

Effects of the Experimental Fluctuating Flows from Glen Canyon Dam in 2003 and 2004 on the Early Life History Stages of Rainbow Trout in the Colorado River

Final Report

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Executive Summary

An experimental alteration of the hydrograph from Glen Canyon Dam (GCD), targeted at reducing the survival rate of young rainbow trout through increased daily fluctuations in flow, was implemented from January through March in 2003 and 2004. This report describes the impact of the experimental flow regime on the early life stages of rainbow trout below Glen Canyon Dam. The study consisted of five components. We measured the timing of redd excavation and the distribution of redds across elevations (i.e., redd hypsometry) in Glen Canyon to estimate the potential egg and alevin mortality caused by the experimental flow regime. We quantified the relationships between spawning habitat preference and depth, velocity, and substrate in Glen Canyon to evaluate the feasibility of controlling spawning elevations through changes in discharge. We obtained monthly samples of Young-of-Year (YoY) from Glen Canyon to compare length-frequencies over time and among habitat types to make qualitative inferences regarding the seasonal timing of hatch, and YoY survival, growth, and movement among habitat types. We analyzed the microstructure of otoliths from a subsample of fish to establish length-age relationships and evaluate the effects of dam operations on YoY growth. These data were used in a stock synthesis model to estimate seasonal trends in the number of rainbow trout emerging from the gravel, and their subsequent survival rates and movement among habitat types. Finally, we conducted rainbow trout spawning habitat, redd, and fry surveys from Lees Ferry to the confluence of the Little Colorado River (LCR) to evaluate the extent of natural reproduction in this reach.

There was minimal spawning prior to mid-January in both 2003 and 2004 and peak counts of approximately 1,000 redds were obtained by late-March/early-April. We estimated that 4,000 and 2,100 redds were excavated in 2003 and 2004, respectively. The average percentage of redds above 12, 8, and 5 kcfs at high elevation spawning sites was 27%, 54%, and 82%, respectively. The system-wide redd survey documented a total of 27 spawning locations in the Glen Canyon with the majority of redds located at elevations below 8 kcfs. Intergravel water temperatures at Four Mile and Powerline Bars increased with elevation and exceeded the lethal egg incubation limit of 16 C by mid-March at higher elevations. Estimates of the percentage of redds that did not produce viable young for Glen Canyon were 23% and

33% in 2003 and 2004, respectively. Mortality in 2004 was higher because of the implementation of a daytime Sunday steady flow of 8 kcfs between January and March. Under normal Record of Decision (ROD) operations from January to March with a similar total volume released from Glen Canyon Dam (GCD) to the volumes in 2003 and 2004, the model predicted a redd loss of 19% in January and 33% from February to March when the majority of spawning occurs. Thus, there was likely very little additional incubation mortality associated with the higher experimental fluctuations in January to March of 2003 and 2004. We estimated that between 1988 and 1991, when daytime low flows during the spawning and incubation period averaged 1-3 kcfs, total redd loss likely exceeded 75%. We predicted that redd loss rates could be increased to over 50% if a daytime Sunday steady flow of 5 kcfs was implemented.

The spawning habitat preference models we developed for rainbow trout in Glen Canyon were useful for evaluating the extent to which increased discharge during the January to March experimental flow period altered the elevations where spawning occurred. Depths of 0.5 – 1.5 m, velocities of 0.3 – 1 m/sec, and D85 values of 15-45 mm were preferred. Weighted useable area computations showed that higher discharges increased total spawning habitat availability at sites that had spawning habitat located at higher stages such as Four Mile and Powerline Bars, and reduced spawning habitat availability at deep-water redd sites such as Ferry Swale. The model also showed that the stages of preferred suitable spawning habitat at Four Mile and Powerline Bars were increased under higher discharges. Such changes in spawning habitat availability would increase the proportion of redds that would be dessicated and increase the duration of exposure. The redd hypsometry study showed that there was a significant proportion of redds excavated in deep-water that would not be dewatered at flows as low as 5 kcfs. The large decline in spawning habitat availability at Ferry Swale under high discharge suggests that spawning at deep-water sites could be suppressed through maintenance of high flows through the entire spawning period; however this conclusion needs to be validated by direct field observations. This uncertainty is important as 40-50% of the redds in Glen Canyon were located below 5 kcfs.

Seasonal changes in length frequencies of YoY in Glen Canyon showed effects of hatch timing, growth, survival variation, and movement from low to steep angle shorelines. Substantial decreases in density following the early-September reduction in the minimum daily flow from 10 to 5 kcfs were observed in both 2003 and 2004, and a very big drop in density in steep angle habitats following the November 2004 42.5 kcfs beach habitat building flow was also seen. Catch rates obtained at the minimum daily flow were 3- to 5-fold higher compared to those during the daily maximum and these differences were statistically significant. A weekly striping pattern was evident in at least 51% of the 255 otoliths examined in 2003 but in only 5% of the 334 otoliths in 2004. The atypical weekly increment was 25% wider compared to the other increments and indicated enhanced growth during Sunday steady flow periods. There was little weekly striping in 2004 because daytime flows were not steady on Sundays during the summer of 2004. Age determinations based on analysis of otolith microstructure were made from 237 and 318 fish in 2003 and 2004, respectively. Variation in length-at-age was very low with logistic growth models predicting 86-87% of the variation in forklength as a function of the number of days from hatch. YoY in steeper habitats were significantly larger at age than those in low angle habitats for fish that were at least 3 months old. Hatch date distributions for the total YoY catch in 2003 (n=966) and 2004 (n=4,647) were computed by length back-calculation. The correspondence between the back-calculated hatch date distributions and those inferred from redd counts was very strong, indicating that there was limited variation in mortality rates over the incubation period. The observation that YoY generally remain at the daily minimum flow elevation, and the post-September density reductions documented in Glen Canyon, coupled with the substantial literature on stranding impacts, support the need to evaluate a 'stranding' flow operation from GCD targeted at reducing YoY recruitment.

Estimates of YoY weekly survival rate from the stock synthesis model in both low and steep angle habitats were approximately 0.85 and were not dependent on the form of the hatch timing distribution. The constant and variable survival rate models provided good fits to the length frequency data and the improved fit of the latter models was useful in untangling recruitment and survival effects in the length frequency data. Survival rates for the period between the August and September samples for low and steep angle habitats of 0.84-0.85

were significantly lower than in the previous (0.91 and 0.95) and following intervals (0.87 and 0.90). This change may have been caused by the reduction in the daily minimum flow from 10 to 5 kcfs in early-September. However, it is also possible that the decrease in survival we estimated was a natural occurrence, possibly driven by a normal ontogenetic habitat shift and/or density-dependent mortality. In steep habitats, weekly survival rates dropped from 0.90 for the period spanning early-September to early-November, to 0.59 for the period between November and December. This change was likely related to the 42.5 kcfs Beach Habitat-Building Flow (BHBF), although it could also have been caused by a natural or flow-induced habitat shift rather. Uncertainty in survival rate estimates was generally larger in low angle habitats because of lower sample size. Hatch timing-patterns estimated from the model were highly uncertain when survival rates were allowed to vary among sample periods. The juvenile stock synthesis modeling approach we have developed represents a potential advance in monitoring the response of salmonid populations to habitat alterations. However, we caution that it does not replace the need to track trends in the adult population. Without this supporting data, it will be uncertain whether a measured change in the mortality at an early juvenile stage will be compensated by a subsequent change in density-dependent mortality.

Exposed gravels and cobbles above 8 kcfs were generally much too coarse and poorly sorted to support spawning between Lees Ferry and the confluence with the Little Colorado River. We observed a handful of very small areas ($10\text{-}400\text{ m}^2$) that contained appropriate grain sizes for spawning, however no redds were observed at any of these locations. Due to high turbidity we were unable to survey for spawning habitat or redds in Marble Canyon below the daily minimum flow elevation of 8 kcfs on the April 2004 trip. In June 2004 water clarity was adequate and suitable spawning substrate below 8 kcfs was found at a number of locations in Marble Canyon, with the majority of larger sites located between the confluence of Nankoweep Creek and Kwagunt rapid (river miles 52 and 56, respectively). The vast majority of these sites were located at the downstream end of riffles or small rapids at depths of 3-10 m at a discharge of ca. 9 kcfs. Nankoweep Creek was accessible to fish in the Mainstem Colorado River in 2004 and could support at least a few thousand spawners between January and early-February when water temperatures are suitable. We did not catch

any young-of-year rainbow trout in Nankowep Creek during the April 2004 survey and saw only limited spawning activity.

Relative to Glen Canyon, we found very few YoY rainbow trout between Lees Ferry and the LCR confluence during the June and August 2004 surveys. Across gear types, densities of YoY rainbow trout in Glen Canyon were 12-fold higher than in Marble Canyon in June and 15-fold higher in August. Densities of YoY in Marble Canyon were highest in the 15-mile reach immediately below Lees Ferry and increased between June and August in the first 30 miles downstream of Lees Ferry. Length-at-age and hatch date distributions for YoY trout caught in Glen and Marble Canyons were very similar. These data suggest that the limited number of YoY caught in Marble Canyon in 2004 likely originated from Glen Canyon. The reach between river mile 45 and 60 had the lowest densities of YoY fish of all the reaches in Marble Canyon with only 14 and 4 YoYs caught in June and August, respectively. Although this reach had the greatest amount of spawning habitat in the mainstem and a tributary that could support a substantial amount of spawning (Nankowep Creek), these habitats clearly did not produce a significant number of viable young in 2004.

If our surveys in Marble Canyon are representative of reproductive conditions for rainbow trout in future years, it is unlikely that flows from GCD can be used to reduce the survival rate of young trout in this reach. There was virtually no spawning habitat above 8 kcfs that could potentially be dewatered. The limited area of spawning habitat that was observed was well below 5 kcfs. The very low densities of YoY observed in 2004 indicate that recruitment to the Marble Canyon population is already quite low, thus the incremental effect of destabilizing shoreline habitats would be very small. Our results cannot be used to definitively determine the origin of the current population of rainbow trout in Marble Canyon. It is possible that these fish originated in Marble Canyon and that the limited reproduction we observed in 2004 was a unique occurrence. Continued documentation of YoY absence in Marble Canyon over the next few years, combined with observations of a constant or increasing adult population above the mechanical removal reach, would provide strong evidence that this population is supported by downstream dispersal from Glen Canyon. Alternatively, if downstream dispersal is not a significant process, and if the lack of local

reproduction in Marble Canyon continues, the rainbow trout population in this reach should decline substantially over the next few years.

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1.0 Introduction

Predation and competition by non-native salmonids has been identified as a potentially important factor contributing to the continued decline of humpback chub and other native fishes in the Colorado River in Grand Canyon (Valdez et al. 1998). To test this hypothesis, members of the Glen Canyon Dam (GCD) Adaptive Management Workgroup elected to actively reduce the abundance of rainbow trout in Grand Canyon through a combination of mechanical removal and changes in discharge. A large-scale mechanical removal program was initiated in January 2003 to reduce salmonid fish densities in a 16-mile section of the Colorado River near the confluence of the Little Colorado River (LCR) that is extensively used by the largest humpback chub aggregation in Grand Canyon (Fig. 1.1). An experimental alteration of the hydrograph from Glen Canyon Dam, targeted at reducing the survival rate of rainbow trout through increased daily fluctuations in flow, was implemented in January through March 2003 and 2004.

The experimental hydrograph consisted of increasing the maximum daily range in flows from a normal range of approximately 7–12 kcfs to 5-20 kcfs (Fig. 1.2). The flow regime exceeded both the maximum daily flow fluctuation and the ramping rates specified in the Glen Canyon Dam Record of Decision (ROD; DOI 1996). The increased fluctuations in flows were mainly intended to reduce the growth and survival of Young-of-Year (YoY) trout in the Marble Canyon reach between Lees Ferry and the LCR confluence (Fig. 1.1) by destabilizing shoreline habitat. Depending on the timing of spawning, the increased fluctuations could also affect incubation success. High flows would increase the elevations where rainbow trout spawn and reduced flows would increase the mortality rate of eggs and alevins in redds that were dewatered. A reduction in the maximum daily discharge on April 1 to ca. 12 kcfs would strand all surviving egg deposition above this elevation.

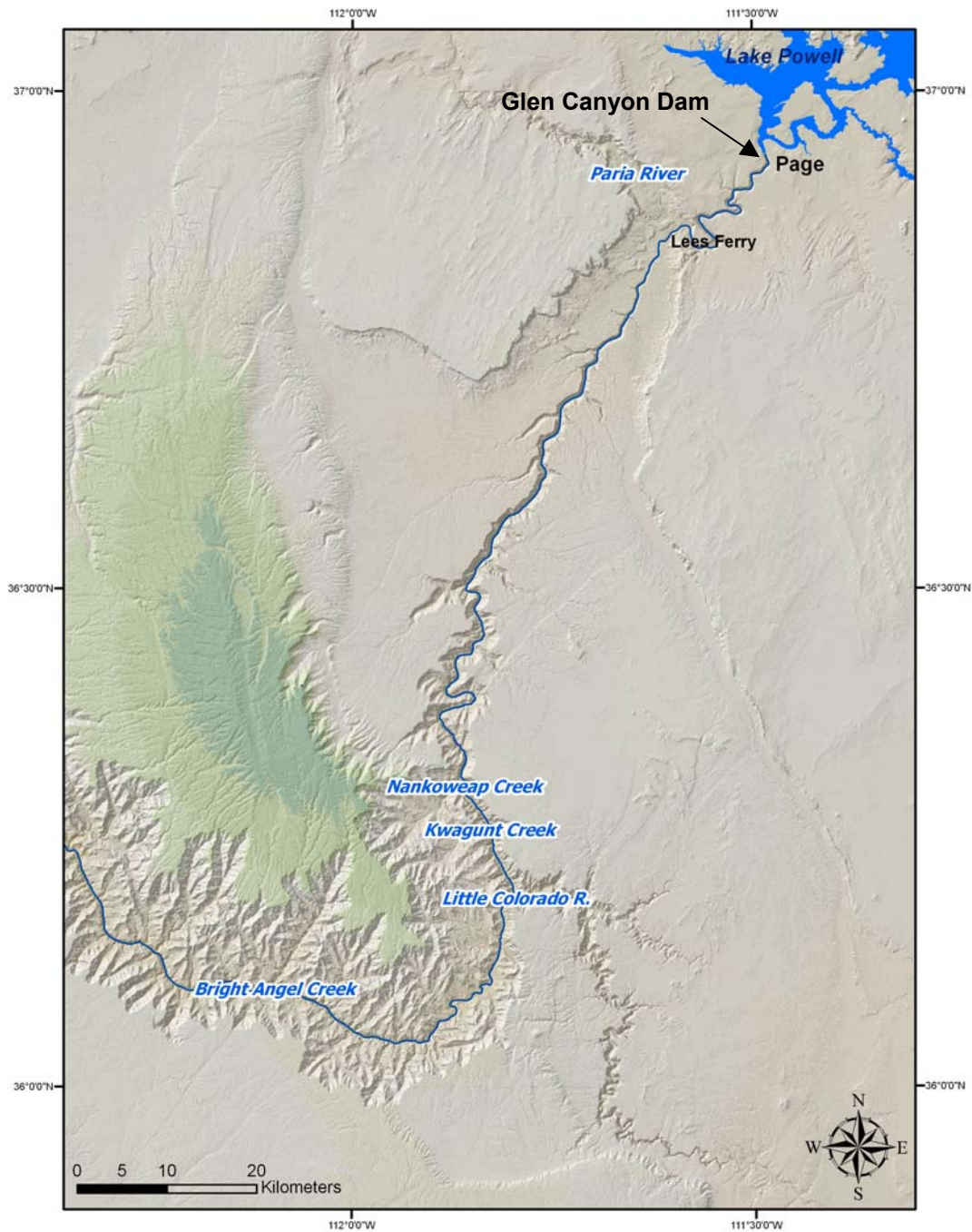


Figure 1.1. Map of the upstream one-third of the Colorado River Ecosystem in Grand Canyon with details of the study area. The section of river between Glen Canyon Dam and Lees Ferry is referred to in the text as Glen Canyon or the Lees Ferry reach. The section of river between Lees Ferry and the LCR confluence is referred to as Marble Canyon.

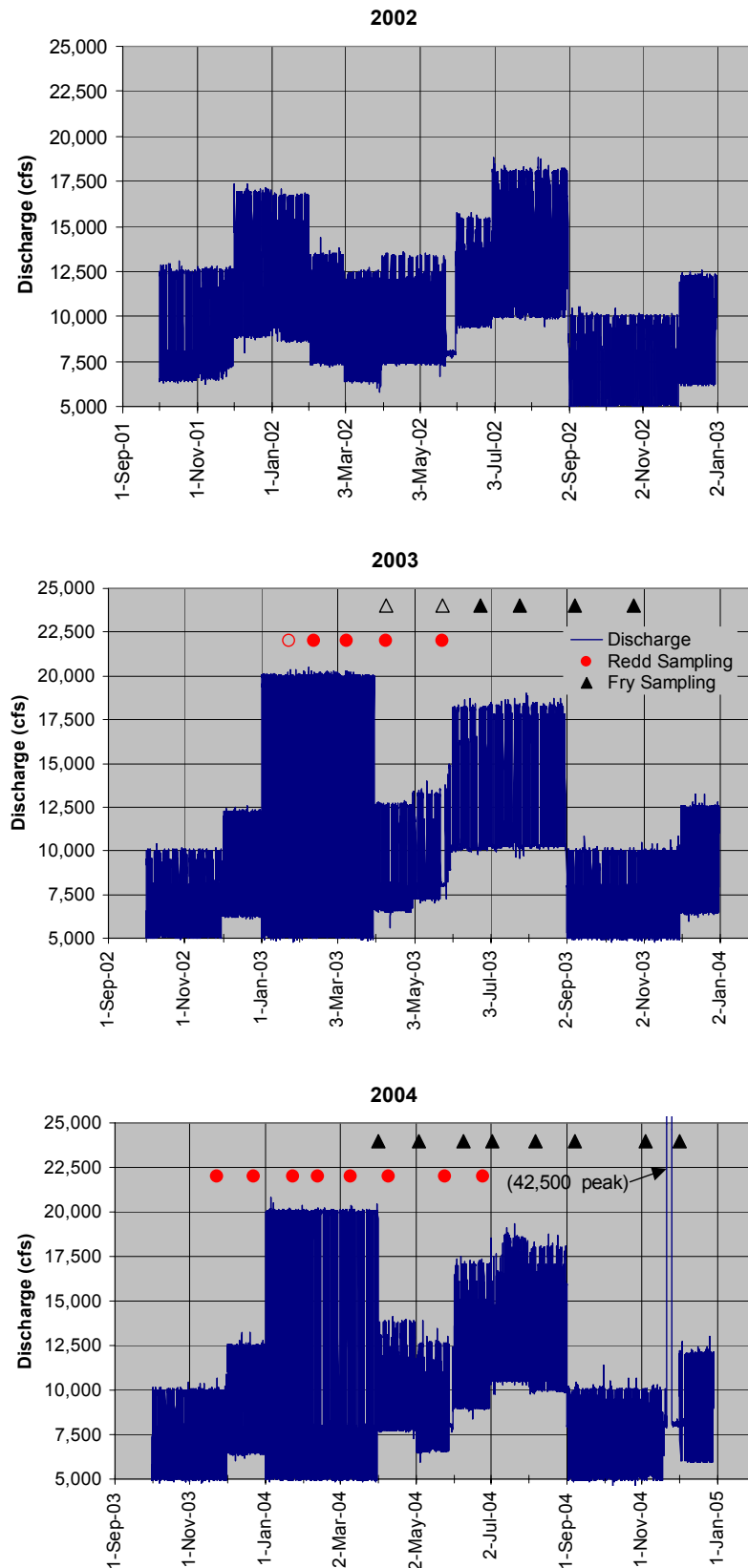


Figure 1.2. Hourly discharge time series from October 1, 2001, through December 31, 2004. Redd and YoY sample periods in 2003 and 2004 are shown by symbols, with open symbols denoting pilot sampling.

This report presents the results from a 2-year field effort designed to assess the effects of the 2003-2004 experimental flow regime on early life stages of rainbow trout. The work was conducted predominantly in Glen Canyon, with limited sampling in Marble Canyon in 2004. Our emphasis in Glen Canyon was motivated by many factors. The fishery for rainbow trout in Glen Canyon is a valuable resource and understanding how operations from Glen Canyon Dam affect it is highly relevant to the overall GCD Adaptive Management Program. Reducing the production of young fish in Glen Canyon, coupled with providing flows that enhance the growth of adult fish, would likely increase the size of catchable fish and is a potentially useful management tool. Many of the methods designed to meet the objectives of this project have never, or only rarely, been attempted in a river system as large as the Colorado River. We elected to conduct the first year of the study in Glen Canyon due to its logistical advantages. We felt that some of the understanding concerning effects of Glen Canyon Dam on the early life stages of rainbow trout in Glen Canyon would be transferable to the population in Marble Canyon. Finally, juvenile or adult rainbow trout emigrating from Glen Canyon may be an important source of recruitment to the population in Marble Canyon. If this is the case, understanding the impacts of dam operations on the recruitment and survival of young rainbow trout in Glen Canyon is highly relevant to understanding how operations effect the population downstream.

Our study consisted of five components. First, we measured the timing of redd excavation and the distribution of redds across elevations (i.e., redd hypsometry) in Glen Canyon, and combined with data on intergravel water temperatures, used a simple model to estimate the potential egg and alevin mortality caused by the 2003-2004 experimental flow regime (Section 2). Second, we quantified the relationships between spawning habitat preference and depth, velocity, and substrate to evaluate the feasibility of controlling spawning elevations through changes in discharge. These relationships were also used to evaluate the potential for rainbow trout spawning in the mainstem Colorado River below Lees Ferry (Section 3). Third, we sampled YoY in Glen Canyon on a monthly basis to compare length-frequencies over time and among habitat types to make qualitative inferences regarding hatch timing, survival, growth, and ontogenetic habitat

shifts. We analyzed the microstructure of otoliths from a subsample of fish to establish length-at-age relationships to evaluate the effects of dam operations on YoY growth. The combined catch and age information were used to back-calculate a hatch date distribution that was compared with the distribution estimated from redd counts and the egg mortality model to look for evidence of differential mortality during the incubation period (Section 4). Fourth, we developed a stock synthesis model to estimate hatch timing, apparent survival rate, and movement of YoY among habitat types in Glen Canyon based on length frequency and age data. Estimates of hatch magnitude and YoY survival from this model can be compared across years under different flow regimes from Glen Canyon Dam to quantitatively evaluate the extent to which operations affect the apparent survival rates of young fish. The procedure also has the potential to help evaluate the effects of dam operations over shorter time-scales (Section 5.). Finally, spawning habitat assessments, and redd and fry surveys in Marble Canyon, were compared to those in Glen Canyon to evaluate the extent of natural reproduction in this reach which will in turn determine the potential to reduce this production through changes in dam operations (Section 6). Information from all components of the study were used to provide a series of recommendations for future experimental flows and monitoring targeted at controlling and assessing the production of young rainbow trout in Glen and Marble Canyons.

2.0 Redd Hypsometry and Timing

Evaluating the effects of the 2003 and 2004 experimental fluctuating flows on the survival of rainbow trout eggs and alevins incubating in gravel substrates in Glen Canyon requires information on intergravel water temperatures and the seasonal timing and hypsometry of spawning. Redd hypsometry is defined as the proportion or number of redds excavated at specific elevation ranges (e.g. between 5 and 8 kcfs). The interaction between spawn timing and monthly flow regimes will determine the fraction of redds potentially effected by experimental fluctuating flows. Within that fraction, redd hypsometry determines the extent of egg and alevin mortality caused by exposure- and temperature-induced impacts.

There is a considerable body of literature documenting the effects of fluctuating flows on the eggs and alevin stages of salmonids. Several studies have shown that salmonid eggs can tolerate long periods of dewatering. Reiser and White (1983) found that eggs dewatered for as long as 4 weeks (steelhead) and 1-5 weeks (chinook) showed essentially no effect on hatching success, or on the development and growth rate of alevins and juveniles, provided the sediment moisture content was maintained at 4% or higher. In a laboratory setting, Becker et al. (1982) determined that the pre-hatch phases of chinook salmon development were tolerant to dewatering but that post hatch alevins were highly susceptible. Reiser and White (1983) cited the proximity of the redd to local ground water as one factor that might influence egg survival during dewatering. Chapman et al. (1986) found that flow fluctuations on the Columbia River did not prevent females from building redds and laying eggs above the minimum flow elevation. They found that 85% of the redds constructed above the minimum flow elevation that were subjected to regular dewatering contained live embryos.

Exposure of redds may result in elevated or reduced temperatures that induce lethal or sub-lethal effects on egg and alevin stages. A maximum lethal temperature for rainbow trout eggs of 16-18 C has been well determined from numerous hatchery studies

(Piper et al. 1986, Ford et al. 1995, Oliver and Fiddler 2001) and increased mortality and developmental abnormalities have been shown to occur at temperatures as low as 13 C (Raleigh et al. 1984, Crisp 1981, McEwan and Jackson 1996, Oliver and Fiddler 2001). The effect of minimum water temperature on incubation mortality is not as well defined. The extensive review by Oliver and Fiddler (2001) cite grey literature that shows complete mortality of rainbow trout eggs at temperatures below 3 C. Incubation mortality associated with very high or low temperatures is not simply a function of the absolute temperature but is also dependent on the embryonic stage, the rate of temperature change, and the duration of exposure (Oliver and Fiddler 2001).

Montgomery and Tinning (1993) conducted laboratory and experimental field trials to measure the survival of rainbow trout eggs and alevins in Glen Canyon under fluctuating flows. They found that the moisture content of exposed sediments (9%) was well above the 4% minimum threshold for egg hatching estimated by Reiser and White (1983). In laboratory studies, they found that periods of exposure of up to 12 hrs. had no influence on hatching success, but that total mortality occurred when exposure was 15 hrs. (Table 2.1). Alevin survival rates were much more sensitive to exposure, with almost no survival at exposures of 12 hrs. or more. Both field and laboratory studies showed that an exposure period of 6 hrs. reduced alevin survival rates by 50% and that mortality rates from exposure periods as low as 3 hrs. could be as high as 60% if temperatures exceeded 11 C. In the field, an exposure of 10 hrs. resulted in 100% mortality of alevins, while 15 hrs. of exposure was required to cause 100% mortality in the laboratory. The authors suggest that differences in sediment grain size distribution (abundance of finer sediment) and moisture content and temperature regimes were the likely factors causing differences between laboratory and field results. Maddux et al. (1987) compared the emergence rates of permanently watered artificial redds with those that were exposed for 10 hrs. They found that emergence success dropped from 12.0% to 0.6% when redds were dewatered.

In this study we counted redds and surveyed their locations in Glen Canyon from February to May 2003 and from November 2003 to July 2004. The survey information allowed us to quantify redd hypsometry. Redd count data were used as input to a model

to estimate the timing of spawning and the total number of redds excavated over the spawning season. Estimates of spawn timing and hypsometry and measured intergravel temperatures at a range of elevations were integrated into a simple spreadsheet model to predict the extent of redd loss at specific sites, and for the entire Glen Canyon reach resulting from the 2003 and 2004 January to March fluctuating flow experiment. Model analyses were used to examine alternate flow strategies that would increase the extent of incubation mortality.

2.1 Methods for Redd Hypsometry and Timing Study

Both intensive and rapid assessment techniques were used to enumerate redds in the Lees Ferry reach below Glen Canyon Dam. The intensive technique provided precise estimates of redd hypsometry at a limited number of important spawning sites. The rapid assessment technique (RAT) provided a less precise estimate of hypsometry but was applied over all spawning areas that were identified in Glen Canyon (Fig. 2.1). Methods used for intensive and rapid assessment redd surveys are described in Sections 2.1.1 and 2.1.2, respectively. Modelling and analytical methods used to interpret the redd count data and to estimate the extent of incubation mortality are described in Sections 2.1.3 and 2.1.4, respectively.

2.1.1 Methods for Redd Surveys at Intensive Sites

Intensive redd surveys in Glen Canyon were conducted monthly from February to May 2003 (Table 2.2) at Four Mile Bar (FM), Ferry Swale (FS), Powerline Bar (PL), and Pumphouse Bar (PH) and twice per month over the same period in 2004. Ferry Swale was not sampled using the intensive method in 2004 because the 2003 surveys showed that all redds were below 5 kcfs, thus there was no need to use the more time consuming method to provide precise estimates of hypsometry. Criteria used to define active redds included the presence of a pit which was usually composed of a coarse deposit, a sorted finer deposit downstream of the pit (tail spill), appropriate grain sizes (5 – 50 mm), and a

Table 2.1. Summary of survival experiments conducted by Montgomery and Tinning (1993) in the laboratory and in Glen Canyon. All experimental results were conducted at water temperatures < 11 C except the one experiment that is noted.

Experimental Results				
	Exposure (hrs)	Duration (days)	Eggs	Survival Rate (%) Alevins
	3	26	100	100
	3 (>11 C)	26	100	40
	6	16		50
	12	16	100	12.5
	15	13	10	0
Field Results				
Stage (kcfs)	Exposure (hrs)	Duration (days)		Survival Rate (%) Alevins
1	0	22		72
5	6	22		32
10	10	22		0
15	15	22		0

Table 2.2. Mid-trip dates for redd surveys conducted in 2003 and 2004.

Sample Type	Project Year	
	2003	2004
RAT Only		23-Nov-03
RAT Only		21-Dec-03
RAT Only		21-Jan-04
Intensive + RAT	12-Apr-03	4-Feb-04
Intensive + RAT		29-Feb-04
Intensive + RAT		14-Mar-04
Intensive + RAT	10-Mar-03	28-Mar-04
Intensive + RAT	10-Apr-03	18-Apr-04
Intensive + RAT		2-May-04
Intensive + RAT	25-May-03	22-May-04
RAT Only		19-Jul-04

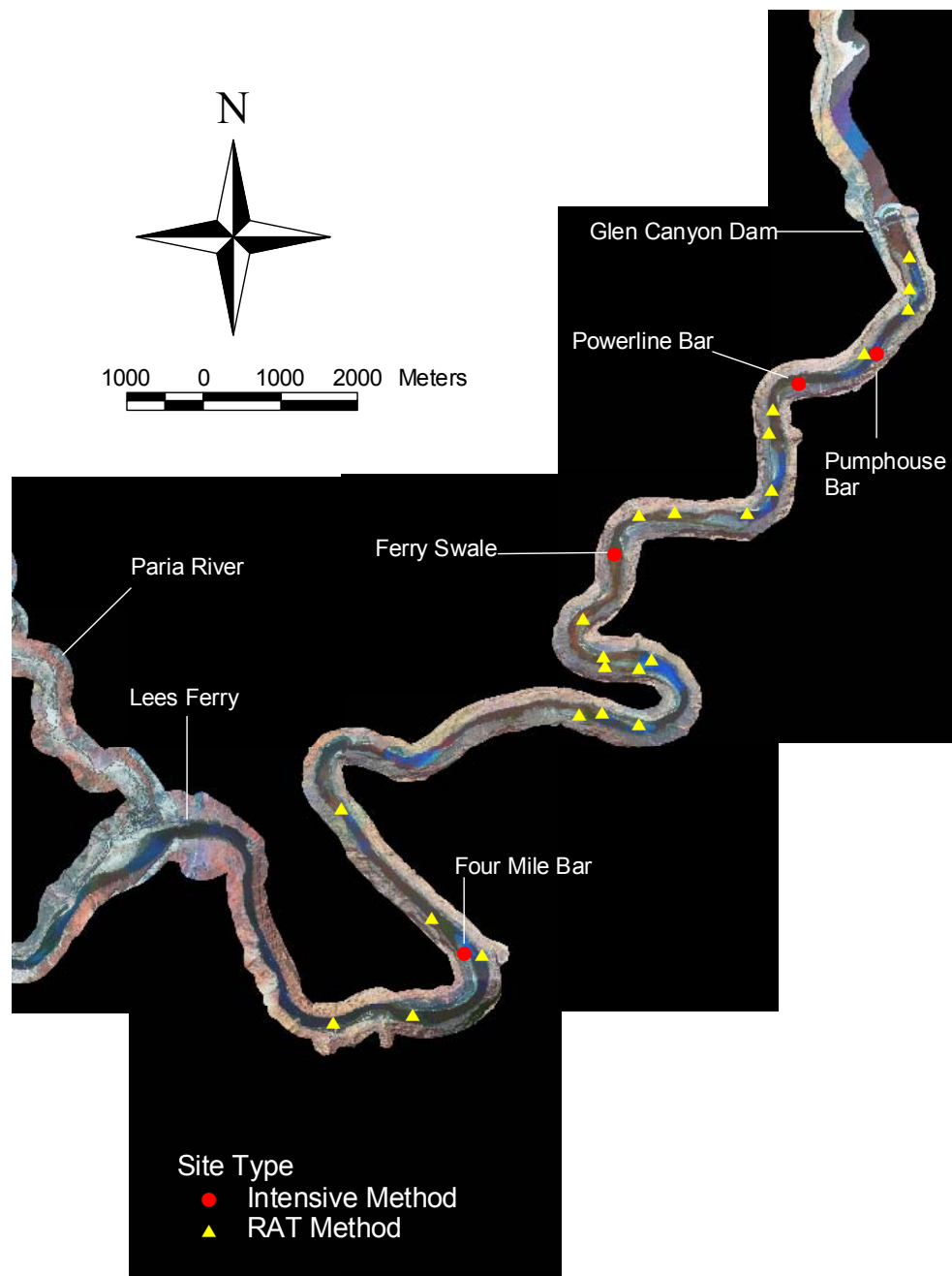


Figure 2.1. Map of Glen Canyon showing locations of intensive and rapid assessment technique (RAT) redd survey sites.

lack of algae, New Zealand mudsnails, macrophytes, or terrestrial vegetation on the sediment in the vicinity of the redds. During the early surveys, a small fraction of redds were excavated with a shovel to determine egg presence and ensure that our criteria for identifying active redds were sound. Identification of active redds was likely more accurate when they were exposed or in shallow water ($< 1\text{ m}$). In deeper water, the presence of fish exhibiting spawning behaviours was used to help identify active redds. Redd surveys were conducted by systematically traversing each site by foot or boat at the minimum daily discharge. At sites where redd densities were high, spray-painted rocks were used to mark redds so they were not double-counted. These rocks were removed at the end of each survey. All redds that met our criteria were counted at every site on each survey.

Redd locations were surveyed with an electronic total station equipped with a digital data collector. A survey rod was placed over the central pit of each redd to obtain its position. For deeper redds, elevations were computed by subtracting the total depth of the redd from the surveyed elevation of the water surface. Total depth was measured using a Lowrance depth-sounder mounted on a 7 m aluminum hulled motorized boat. The boat was spatially referenced with the total station by targeting a prism cluster mounted on a mast directly above the transducer. Point data were referenced to the Arizona State Plane NAD83, Arizona Central (FIPS 202) coordinate system, in meters, using benchmarks within a previously established control network. Survey accuracy in the field was maintained by horizontal and vertical checks of positional error between known reference points. Upon completion of each survey, field data were edited for spurious rod heights and miscodes. Ground point data had a positioning accuracy of better than 0.05 m and vertical accuracy that varied from 0.03 to 0.05 m. Point data collected from the boat had a positioning accuracy of better than 0.5 m and a vertical accuracy of 0.25 m or less.

Stage-discharge relationships were empirically developed for each site and used to translate surveyed redd elevations into their discharge equivalents. Water elevations were surveyed at 5, 8, 12, 15, and 20 kcfs at each site. Measurement of water surface elevation was almost always done at steady discharges, which allowed us to assume that

discharge at the site was equivalent to the discharge from Glen Canyon Dam at the time of the survey. In the few cases when survey measurements were conducted at unsteady discharge, we routed the relevant portions of the Glen Canyon Dam discharge record to the location of the study sites using a one-dimensional unsteady flow model (Wiele and Griffin 1997). Under unsteady flow, only data within 2 kcfs of the targeted discharges (5, 8, 12, 15, and 20 kcfs) were used in the estimation of the stage-discharge relationships. A 2nd order polynomial was fit to the stage-discharge data (Fig. 2.2). The morphology and large size of Four Mile Bar required the development of two independent stage-discharge relationships for the upper and lower bars. Surveyed redd locations and habitat measurements were assigned to the appropriate relationship by overlaying their locations on the polygons that defined the areas for each stage-discharge relationship.

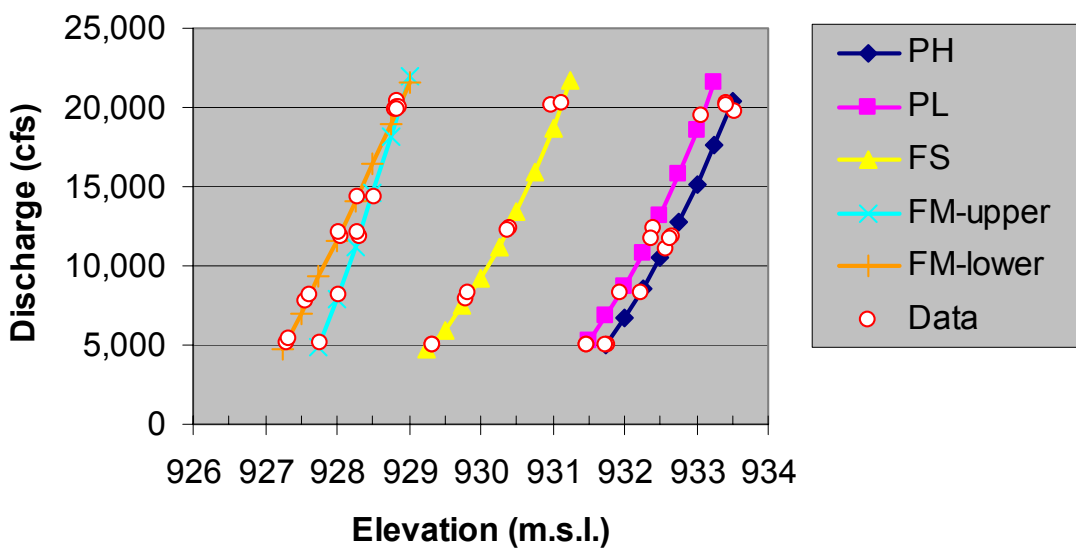


Figure 2.2. Stage-discharge data (circles) and best-fit relationships at Pumphouse Bar (PH), Powerline Bar (PL), Ferry Swale (FS), and Four Mile Bar (FM-upper, FM-lower).

Continuously recording temperature loggers were buried in the gravel at a depth of 15 cm (Kondolf 2000) at 5, 10, 12, 15, and 18 kcfs at Four Mile and Powerline Bars between February and May 2003 and 2004. Loggers were deployed along a transect

perpendicular to the longitudinal axis of the river with two transects per site. Temperature loggers recorded instantaneous temperature at a one-hr. interval.

2.1.2 Methods for Rapid Assessment Technique (RAT) Redd Surveys

Intensive sites were chosen because they were historically important spawning sites that likely contained a significant proportion of the total number of redds excavated in Glen Canyon. However, these sites were not necessarily representative in terms of the timing of redd excavation or hypsometry. We used a “rapid assessment technique” (RAT) survey during the March, April, and May sampling sessions in 2003 and from November 2003 through July 2004 to derive less precise but system-wide estimate of redd numbers and hypsometry (Table 2.2). Surveys were conducted by foot and by boat typically during steady flows. A clear-bottomed kayak towed from a boat was used to count redds when depths exceeded 1 meter.

On each survey we visited all historical spawning locations (M. Yard, GCMRC, unpublished data as presented in Foster 2002) and examined additional locations that had potential spawning habitat. The height of redds above the water surface was estimated using an Abney or laser level mounted to a survey rod. The depth of submerged redds was measured with either a survey rod or a depth sounder. If discharge from Glen Canyon Dam was not steady at the time of the survey, we used an unsteady flow model (Wiele and Griffin 1997) to predict discharge at each site at the time of the survey. The elevation of the water surface was estimated using the discharge at the time of the survey and the nearest stage-discharge relationship from the STARS model (Randle and Pemberton 1987). Redd elevations were computed by adding the height of the redd relative to the water surface to the elevation of the water surface. Redd elevations were then translated into their discharge-equivalents using the same STARS stage-discharge relationships.

2.1.3 Redd Count Model

The total numbers of redds and the timing of excavation over the spawning season can be estimated from repeated redd counts using an Area-Under-the-Curve (AUC) approach (Irvine and Nelson 1995). The traditional AUC implementation involves plotting the number of redds counted per survey as a function of time (e.g., weeks from the onset of spawning) and generating a curve using linear interpolation. The integral, or total area-under-the-curve, determines the number of redd-weeks, which is in turn divided by an estimate of redd survey life (SLR in units of weeks) to determine the total number of redds excavated (E) over the season,

$$(2.1) \quad E = \frac{AUC}{SLR}.$$

Survey life is the time required for a redd to lose the characteristics that we used to classify it as an active redd. Survey life will be determined by a number of factors including the residence time of spawning fish on the redd, substrate characteristics, slope, bar traffic (anglers), and inundation frequency. If survey life is longer or equal to the length of time between the start and end of spawning and there is no redd superimposition, the peak redd count will be equivalent to the total number of redds excavated over the season. However, if survey life is shorter than the duration of the spawning period, the total number of redds that are excavated will be higher than the peak count. In the case of rainbow trout spawning in Glen Canyon, where redd residence time is on the order of 1-2 weeks, and where a significant amount of spawning occurs over a period of months, the total number of redds excavated will be considerably higher than the peak redd count.

The AUC method has a few significant limitations:

1. It is difficult to characterize uncertainty in the estimate of the total number of redds;

2. An arbitrary assignment of the beginning and ending spawning dates is required if the first and last surveys have non-zero counts; and
3. It does not explicitly take into account spawn timing, and is therefore not useful for determining the proportion of redds excavated between certain dates.

All issues, especially 3, are highly relevant in the case of evaluating the impacts of the January to March 2003-2004 experimental flows. More recently, maximum likelihood methods have been used to fit migration- or spawn-timing models to periodic count data in order to estimate escapement (Hilborn et al. 1999, Korman et al. 2002). These models overcome all three weaknesses of the AUC-method described above and are highly applicable to estimating the timing of rainbow trout spawning in Glen Canyon.

We used Hilborn et al.'s (1999) approach to predict the magnitude and timing of redd excavation in Glen Canyon based on periodic redd counts and an estimate of redd survey life. The total number of redds observed on any week (RP_t) was predicted based on the equation,

$$(2.2) \quad RP_t = A_t - F_t,$$

where, A_t is the cumulative number of redds excavated up to and including week t , and F_t is the cumulative number of redds that have 'faded', that is, are no longer considered active by an observer because they have exceeded their survey life.

The timing and magnitude of redd excavation was modeled using a Beta distribution,

$$(2.3) \quad A_t \propto E \int_0^t \theta_t^{(\alpha-1)} (1-\theta_t)^{(\beta-1)} dt,$$

where E is the total number of redds excavated over the spawning season, and α and β are parameters of the beta distribution that define the timing of spawning. θ_t represents the proportional date of the run and ranges from 1/52 on the first week to 1 on the last

week (T), that is $\theta_t = t/T$. Note that the form of the Beta distribution in eqn. 2.3 returns the cumulative frequency (i.e., the total number of redds excavated up to week t) so the number of redds excavated on week t is $A_t - A_{t-1}$. We modeled the cumulative number of redds that exceeded their survey life on week t as,

$$(2.4) \quad F_t = A_{ct-SLR},$$

where SLR is redd survey life in units of weeks. Note that survey life should include the effects of both natural ‘fading’ and redd superimposition. Given an AUC derived from periodic redd counts, the estimate of the total number of redds excavated over the spawning period should increase with the rate of superimposition due to a decrease in redd survey life. However as described below, our method for estimating survey life cannot account for superimposition and therefore represents a maximum value, leading to a minimum estimate of the total number of redds that were excavated.

The total number of redds excavated over the spawning season (E) and arrival model parameters (α, β) were fit to the observations of redd counts across survey periods. A spatial analysis of redd count data at intensive sites (described below) was used to estimate redd survey life. Observation error was assumed to be normally distributed. Most-likely parameter estimates (MLEs) were computed by minimizing the sums of squares between the observed and predicted total redd counts over the survey periods. The model was fit to redd count data from specific sites (Four Mile and Powerline Bars) as well as to the combined redd count data from intensive and RAT sites. As we did not conduct a RAT survey in February 2003, we used the ratio of the intensive-to-RAT survey counts in March (1.08) to expand the intensive-site count in February to provide an estimate of the total (RAT + Intensive) count.

A spatial analysis of the redd survey data from intensive sites was used to estimate redd survey life. From the AUC method, the total number of redds that are created over a defined period is the ratio of the area-under-the-curve between two survey dates that span this period and the survey life (eqn. 2.1). We rearranged the AUC

equation to estimate survey life based on the ratio of AUC to the actual number of redds excavated. AUC was determined by linear interpolation of the redd count data while the actual number of redds excavated was determined from a spatial analysis. Each intensive survey site was divided into a grid of 1-m² cells using a Geographic Information System (GIS). The presence or absence of redds in each cell on each survey period was then computed. The number of cells which contained a redd on survey x but did not on the previous survey ($x-1$) provided a minimum estimate of the actual number of ‘new’ redds deposited between the two surveys. Summing the number of cells that contained only ‘new’ redds across all surveys provided a minimum estimate of the total number of redds that were excavated. The number of cells which contained a redd on survey $x-1$ but not on survey x provided an estimate of the number of redds lost due to fading as they exceeded their survey life. The number of cells with a redd present in two consecutive sampling periods provided an estimate of ‘old’ redds, that is, redds counted on survey x that were also present on survey $x-1$. The combined total number of cells with ‘new’ and ‘old’ redds was used to compute the number of redds present at-a-site on any survey which would be equivalent to the number that was counted as long as there is not more than one redd per 1-m² cell. We computed the AUC between the first and last surveys based on the total of ‘new’ and ‘old’ redds and divided by the estimated number of ‘new’ redds that were excavated over this period to estimate survey life. These calculations were done for all intensive survey sites sampled in 2003 and 2004. Our estimates of survey life should be considered maximum values as the denominator for this computation, the number of ‘new’ redds, will be underestimated due to redd superimposition. As the rate of superimposition increases, so does the extent of negative bias in the denominator, that in turn increases the extent of a positive bias in survey life. Resulting estimates of the total number of redds excavated over the spawning season should therefore be considered minimum values.

2.1.4 Redd Mortality Model

We developed a model that integrated the effects of spawn timing, redd hypsometry, temperature-dependent incubation time, and intergravel water temperatures on egg and alevin mortality to predict the number of redds that would not produce viable

young. The model operates on a daily time step and was applied at a site and a system-wide scale. The calculations can be divided into seven components:

1. The predicted number of redds excavated by week over the entire spawning season (November 1 – October 31) estimated by the redd count model (Section 2.1.3) were linearly interpolated to daily values;
2. These redds were distributed across four elevation bands (<5, 5-8, 8-12, 12-15, and 15-20 kcfs) based on the observed hypsometry, which varied on a seasonal basis;
3. Daily average, daily maximum, and daily minimum intergravel water temperatures for each elevation band were computed from hourly temperatures recorded at 5, 10, 12, 15, and 17-18 kcfs. The average of temperature statistics of loggers at 5 and 10 kcfs was used to represent the temperatures in the 5-8 kcfs band. Temperature statistics on the first day the loggers were installed (early February) were used to represent temperatures from November 1st to the date of installation. Temperature statistics on the last day the loggers were retrieved (late May) were used to represent temperatures after this date. These extrapolations had little effect on model results as there was only minimal amounts of incubation prior to or following logger installation;
4. The number of days between spawning and hatching was computed by determining the time required to exceed an Accumulated Thermal Unit (ATU) threshold of 329 degree (C)-days (Jensen et al. 1992). Each combination of spawning date and elevation band potentially had a unique thermal history which in turn determined a unique hatch date;
5. The number of days between hatching and emergence was assumed to be 30 days based on the analysis of otolith microstructure in rainbow trout fry collected in Glen Canyon in 2003 and 2004 (see Section 4.1.2).
6. Maximum and minimum daily temperatures thresholds during the egg (spawn-to-hatch) and alevin (hatch-emergence) incubation periods were derived from the literature. If the maximum daily temperature on one or more days at an elevation band exceeded the maximum threshold, or if the minimum daily temperature on one or more days was below the minimum threshold, redds excavated on that day

within that elevation band were considered to not produce viable young. We used a maximum threshold temperature for eggs and alevins of 16 C, but also simulated more conservative cases where the threshold temperature was 18 and 20 C. We used a minimum incubation temperature of 3 C but also simulated a more conservative case of 0 C.

7. The number of non-viable redds was summed across elevation bands over the entire spawning period to determine the total redd loss.

The fraction of redds distributed by elevation bands (2 above) varied over three time blocks that reflected major changes in monthly discharge regimes in 2003 and 2004 (Fig. 1.2) which were shown to control spawning elevations (Section 2.2): November-December (5-12 kcfs); January-March (5-20 kcfs); and April- May (6-13 kcfs). Hypsometry data collected during the first survey when both intensive and RAT sites were monitored (February) was used to estimate the proportions for the November-December period. The proportion of redds at elevations >12 kcfs in the February samples were greater than zero as some redds were deposited following the onset of the experimental 5-20 kcfs daily regime. However, as flows between November and December did not exceed 12 kcfs, these proportions needed to be set to zero. The proportions in the three bands below 12 kcfs were increased by 1/3rd of the proportion deposited above 12 kcfs so that they summed to one. Redd hypsometry from surveys in March was used to estimate the proportions for the January-March period. Redd hypsometry from May surveys was used to estimate the proportions for the April-June period. As for the November-December proportions, proportions for bands above 12 kcfs were set to zero and the proportions for the lower bands were increased by an equal amount so they summed to one.

2.2 Results from Redd Hypsometry and Timing Study

Redd counts increased as the spawning season progressed and reached peak values of approximately 1000 redds by late-March/early-April in both 2003 and 2004

(Fig. 2.3). The total number of redds at the intensive sites monitored in both years (Four Mile, Powerline, and Pumphouse bars) was a little less than 50% of the total number summed across all sites. Considerably more redds were present in May 2003 compared to May 2004, suggesting either a larger late-run component in 2003 or a change in sampling protocol.

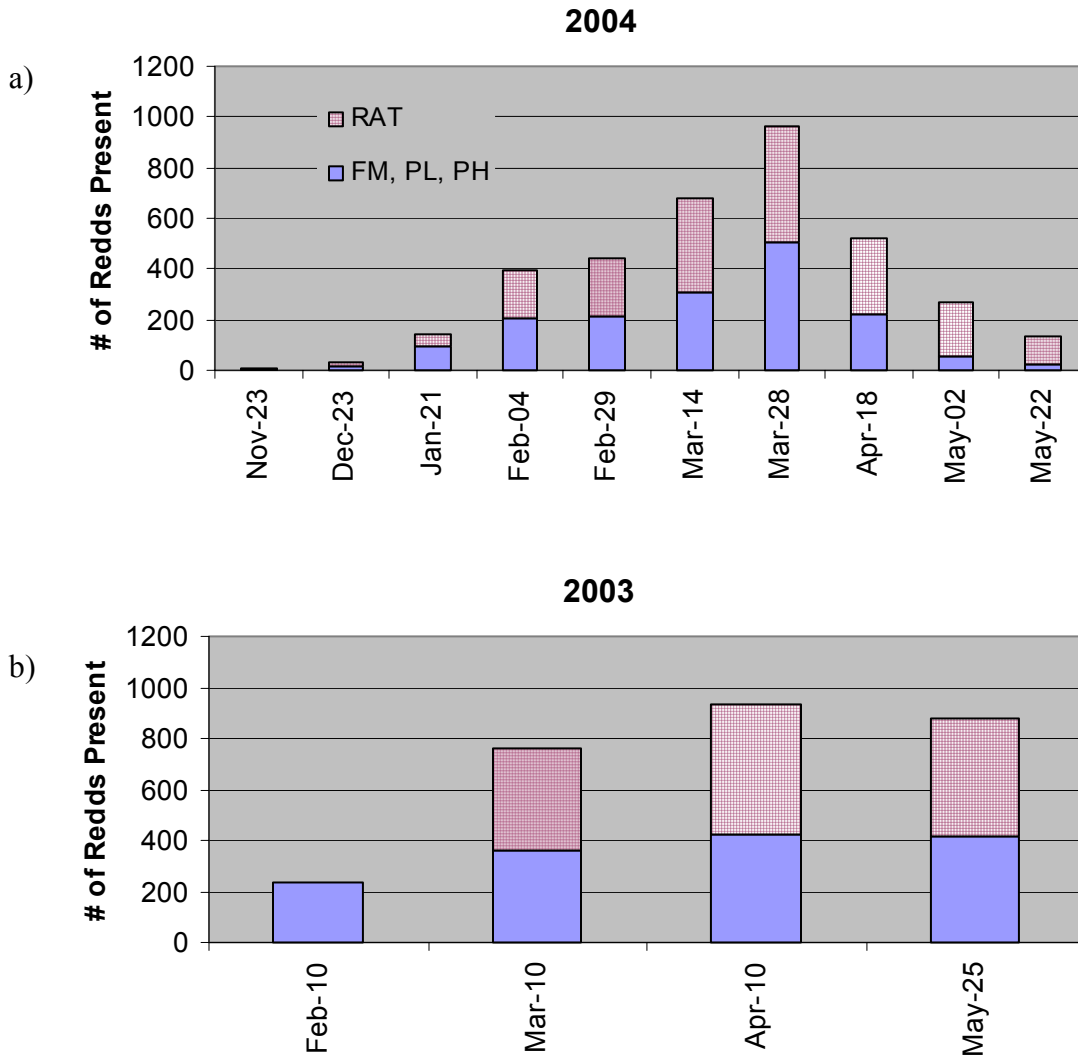


Figure 2.3. Redd counts in a) 2004 and b) 2003 summed across intensive sites monitored in both years (Four Mile Bar, Powerline Bar, and Pumphouse Bar) and the total across all other sites (RAT). A RAT survey was not conducted during the February survey in 2003.

Estimates of redd survey life based on a spatial analysis of redd count data were reasonably consistent across sites within years. The number of 1-m² grid cells that contained redds was very similar to the total number of redds counted, indicating that there were only rare cases when more than one redd was present in a 1-m² cell (Table 2.3). Estimates of survey life based on the ratio of the number of cells with redds present to the number of cells with ‘new’ redds averaged 6.2 weeks in 2003 and 3.7 weeks in 2004 (Table 2.4). Within years, survey life was very consistent among all sites that had a reasonably high proportion of redds that were exposed for part of the day (PH, PL, FM). The relatively fine grain size (pea gravel) and high velocities in the spawning area at Ferry Swale may have resulted in a lower survey life. These redds were also permanently submerged which would have increased the rate of algal recolonization following excavation relative to redds at other sites that were exposed for part of the day. Given these characteristics, redds at Ferry Swale likely faded quite quickly if they were not actively maintained. However, lower survey life at Ferry Swale could also have been caused by sampling error. The locations of redds at Ferry Swale were less precisely determined compared to those at other sites because redds were surveyed from a boat rather than by foot. Reduced precision of redd locations could have resulted in a positive bias in the number of ‘new’ redds, leading to an underestimate of survey life. The extent of bias in survey life resulting from error in redd locations could be evaluated through simulations.

Survey life estimates in 2004 of 3.7 weeks were almost half the value of those estimated in 2003 (Table 2.4). On average, surveys were conducted every 2.5 weeks in 2004 compared to every 5 weeks in 2003. The probability that an existing redd will be superimposed by a new one between surveys increases with the duration between surveys. We were therefore more likely to underestimate the number of ‘new’ redds in 2003 compared to 2004. As survey life is computed from the ratio of AUC to the number of ‘new’ redds, this bias would lead to an overestimate of survey life. We therefore consider the 2004 survey life estimates to be more realistic, and use an average survey life of 4 weeks in the redd count model to determine spawn timing and the total number of redds excavated over the spawning season.

Table 2.3. Summary of spatial analysis of redd count data to determine redd survey life. The number of 1m² grid cells containing redds was summed into the following three categories: New = cells with a redd present in the current, but not previous, survey; Faded = cells with a redd present in the previous, but not current, survey; Old = cells with a redd present in both the previous and current surveys. The number of cells that contained redds (“Present”) is simply the sum of the cells in the “New” and “Old” columns. The column labeled ‘Redd Count’ is the actual number of redds counted on each survey. PH, PL, FS, and FM refer to Pumphouse Bar, Powerline Bar, Ferry Swale, and Four Mile Bar, respectively.

Site & Year	Period	# of 1m ² Cells		Old	New + Old (Present)	Redd Count
		New	Faded			
2004						
FM	Feb 04				142	144
	Feb 04-Feb 29	89	112	30	119	123
	Feb 29-Mar 14	163	79	40	203	211
	Mar 14-Mar 28	271	121	82	353	367
	Mar 28-Apr 18	58	333	20	78	79
	Apr 18-May 02	26	71	7	33	33
	May 02-May 22	18	29	4	22	22
PL	Feb 04				52	54
	Feb 04-Feb 29	39	24	28	67	70
	Feb 29-Mar 14	47	40	27	74	76
	Mar 14-Mar 28	68	40	34	102	110
	Mar 28-Apr 18	30	91	11	41	41
	Apr 18-May 02	9	38	3	12	13
	May 02-May 22	1	12	0	1	1
PH	Feb 04				8	8
	Feb 04-Feb 29	18	5	3	21	21
	Feb 29-Mar 14	14	16	5	19	19
	Mar 14-Mar 28	21	15	4	25	27
	Mar 28-Apr 18	14	22	3	17	18
	Apr 18-May 02	3	13	4	7	8
	May 02-May 22	0	7	0	0	0

Table 2.3. Con't.

Site & Year	Period	# of 1m ² Cells		Old	New+Old (Present)	Redd Count
		New	Faded			
2003						
FM	Feb 10				171	174
	Feb 10-Mar 10	162	109	62	224	230
	Mar 10-Apr 10	214	150	74	288	293
	Apr 10-May 25	212	150	138	350	371
FS	Feb 10				20	20
	Feb 10-Mar 10	34	20	0	34	36
	Mar 10-Apr 10	76	34	0	76	88
	Apr 10-May 25	59	73	3	62	96
PL	Feb 10				42	43
	Feb 10-Mar 10	72	16	26	98	101
	Mar 10-Apr 10	88	81	17	105	105
	Apr 10-May 25	18	84	21	39	41
PH	Feb 10				15	15
	Feb 10-Mar 10	19	9	6	25	26
	Mar 10-Apr 10	17	19	6	23	23
	Apr 10-May 25	3	22	1	4	4

Table 2.4. Statistics used to estimate redd survey life based on a spatial analysis of redd counts across successive surveys. Survey life (in units of weeks) was computed based on the ratio of the integral of the number of redds present over the entire survey period (redd-weeks) to the number of new redds excavated over the same period. PH, PL, FS, and FM refer to Pumphouse Bar, Powerline Bar, Ferry Swale, and Four Mile Bar, respectively.

Site & Year	New Redds	Redd-Wks.	Survey Life (wks.)
2004			
FM	625	2180	3.5
PL	194	816	4.2
PH	70	233	3.3
Avg.			3.7
2003			
FM	588	3919	6.7
FS	169	783	4.6
PL	178	1161	6.5
PH	39	265	6.8
Avg. (all)			6.2
Avg. (except (FS))			6.7

The redd count model was able to provide good fits to the numbers of redds counted across surveys (Fig. 2.4). In 2004, the model estimated that a total of 2,100 redds were excavated with 64% of the spawning occurring between February and March when impacts from dam operations would be most severe. Due to logistical limitations, we were unable to complete a redd survey very late in the season in 2003 and the end of spawning was therefore poorly defined. However, from back-calculation of spawning dates through analysis of otoliths from fry captured in the summer of 2003 where the latest hatch date was precisely determined, there was no evidence of substantial

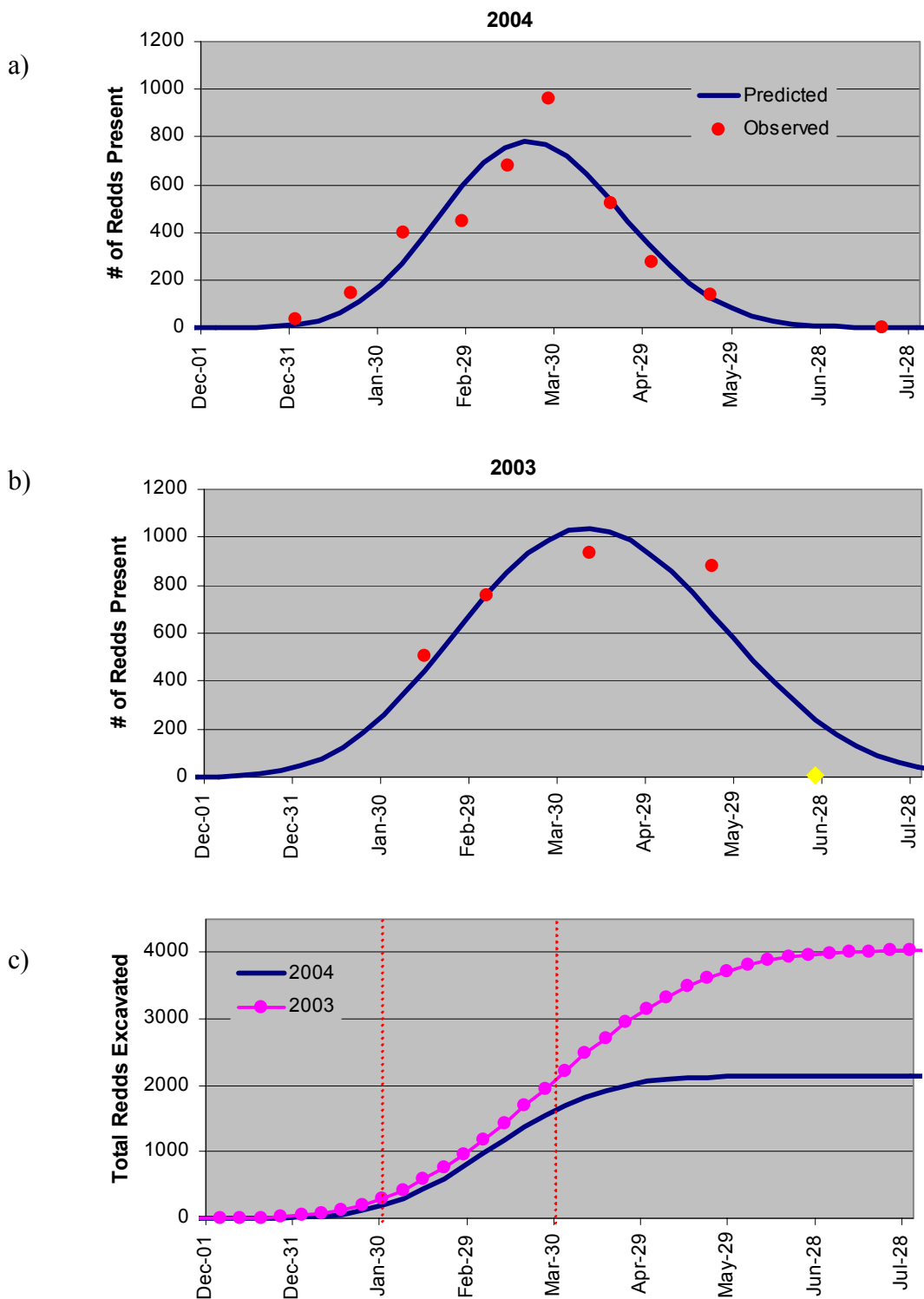


Figure 2.4. Predictions of the number of redds present in a) 2003 and b) 2004 and c) the resulting predictions of the total number of redds excavated based on a survey life of 4 wks. The yellow diamond in b) is the estimated date when no redds would be present based on back-calculation of hatch dates from fry sampling. Redds excavated in February and March, as identified by the area between the vertical lines in c) are the most sensitive to impacts from dam operations.

spawning activity after May (Section 4). Given a redd survey life of 4 weeks, it is quite reasonable to assume that very few redds would have been present by late June if spawning ceased by the end of May. When the model was fit to the 2003 data with this assumption, the estimate of the total number of redds excavated over the entire season was 4,000 with only 41% of the spawning occurring between February and March. The large difference in total redd numbers and spawn timing between 2003 and 2004 was caused by the higher redd counts in April through June of 2003, which in part could have been caused by a change in the protocol used to classify active redds.

The late-March/early-April peak redd count in 2003 and 2004 was about 2 months later than the average spawning peak estimated for the 1990s based on the percentage of ripe fish captured in Glen Canyon by boat electrofishing (McKinney et al. 1999). This shift in spawn timing is consistent with anecdotal observations by the Arizona Game and Fish Department and fishing guides (D. Foster, Marble Canyon Fishing Guides, Marble Canyon, AZ, pers. comm.) that the peak of spawning has moved from early-winter to spring. However, Angradi et al. (1992) used redd counts to estimate a peak in spawning in Glen Canyon between late-March and early-May, a result that is very consistent with our findings. It is difficult to determine whether differences between McKinney et al.'s (1999) and Angradi et al.'s (1992) peak spawn dates are real or are due to differences in methodology. Ripe fish may become progressively less vulnerable to sampling as the spawning season progresses and they move into very localized spawning areas. This dynamic could result in an underestimate in the date of peak spawning based on catches of ripe fish.

The effects of the flow regime from Glen Canyon Dam (Fig. 1.2) on redd hypsometry (Fig 2.5) was apparent in both the 2003 and 2004 data. At Four Mile Bar, the percentage of redds below 8 kcfs dropped from 50% on the first survey in early-February to 25% by late-March (Fig. 2.6). The number of redds at all elevations increased over this time period, but proportionally, there was a much larger increase at higher elevations. High flows between January and March likely promoted spawning at higher elevations. The average percentage of redds above 12, 8, and 5 kcfs across both years and all surveys

at intensive sites (excluding Ferry Swale in 2003) were 27%, 54%, and 82%, respectively. These values are remarkably similar to Angradi et al.'s (1992) estimates of 29%, 59%, and 83% based on surveys at four locations in Glen Canyon (4-, 6-, 9-, and 14- Mile Bars) from December 1990 to April 1991. Note that median daily maximum and minimum flows during this period were 15 and 4 kcfs, respectively and 80th percentile maximum and minimum daily flows were 19 and 5 kcfs, respectively. These ranges are reasonably similar to those during the December to April 2003-2004 spawning seasons.

The system-wide RAT survey documented a total of 27 spawning locations in the Glen Canyon (Table 2.5, Fig. 2.1). There was a strong correlation between peak redd counts by spawning location among years ($r^2 = 0.92$) indicating relatively consistent use. The majority of spawning at more than half of these sites occurred at elevations below 8 kcfs (Fig. 2.7). The proportion of redds below 8 kcfs at RAT sites increased between early-February (60%) and late February (80%) in spite of the fact that maximum daily flows were high over this period. Based on peak redd counts, the largest spawning sites that are below the daytime minimum flow specified in the ROD (i.e., < 8 kcfs) are deep-water sites near the Slough and Honey Draw, Ferry Swale, Duck Island, and 3.5 Mile Bar. The largest high-elevation spawning sites are located at Powerline, 7.5, and Four Mile Bars. There was a considerably higher proportion of redds below 5 and 8 kcfs at RAT sites (Fig. 2.7) relative to the distribution at intensive sites only (Fig. 2.6).

The percentage of redds below 8 kcfs that were deposited during the January to March experimental flow period in Glen Canyon (RAT and intensive sites combined) was about 60% in both 2003 and 2004 (Fig. 2.8). In 2004, this percentage increased to about 90% by the early-May survey suggesting that higher flows between January and March were effective at reducing the percentage of spawn at lower stages that would not be vulnerable to desiccation- and temperature-related mortality from dam operations. Data from 2003 do not support this conclusion as there was no obvious shift in hypsometry between early-April and late-May. This discrepancy may be an artifact caused by differences in redd determinations among years. There were approximately 200 redds at elevations > 12 kcfs by late-March to early-April in both years (Fig. 2.8).

a) Pumphouse Bar

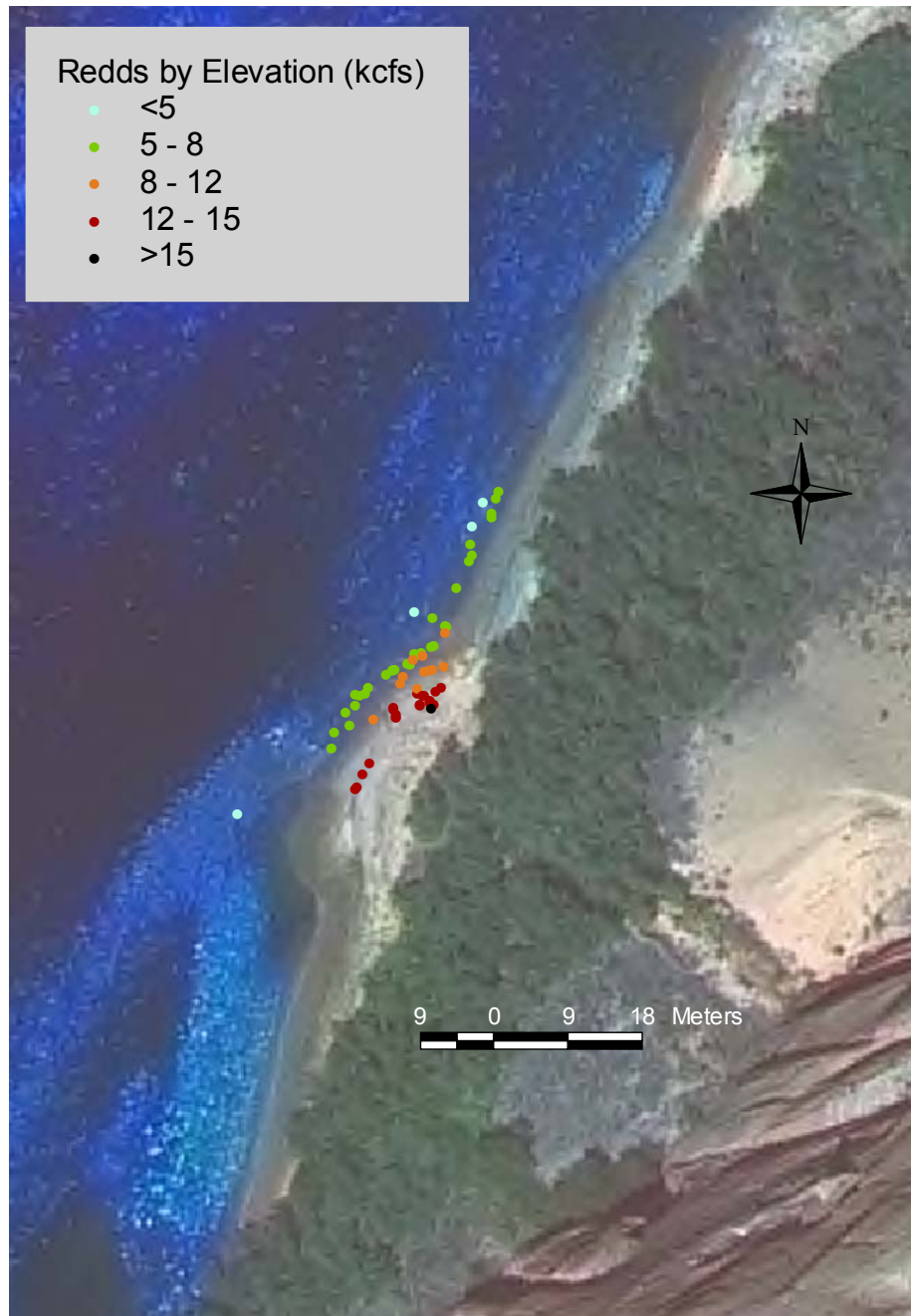


Figure 2.5. Redd location and elevation at a) Pumphouse Bar, b) Powerline Bar, c) Ferry Swale, and d) Four Mile Bar across all four surveys in 2003. Light blue, green, orange, redd, and white circles denote redd elevations <5, 5-8, 8-12, 12-15, and >15 kcfs, respectively.

b) Powerline Bar

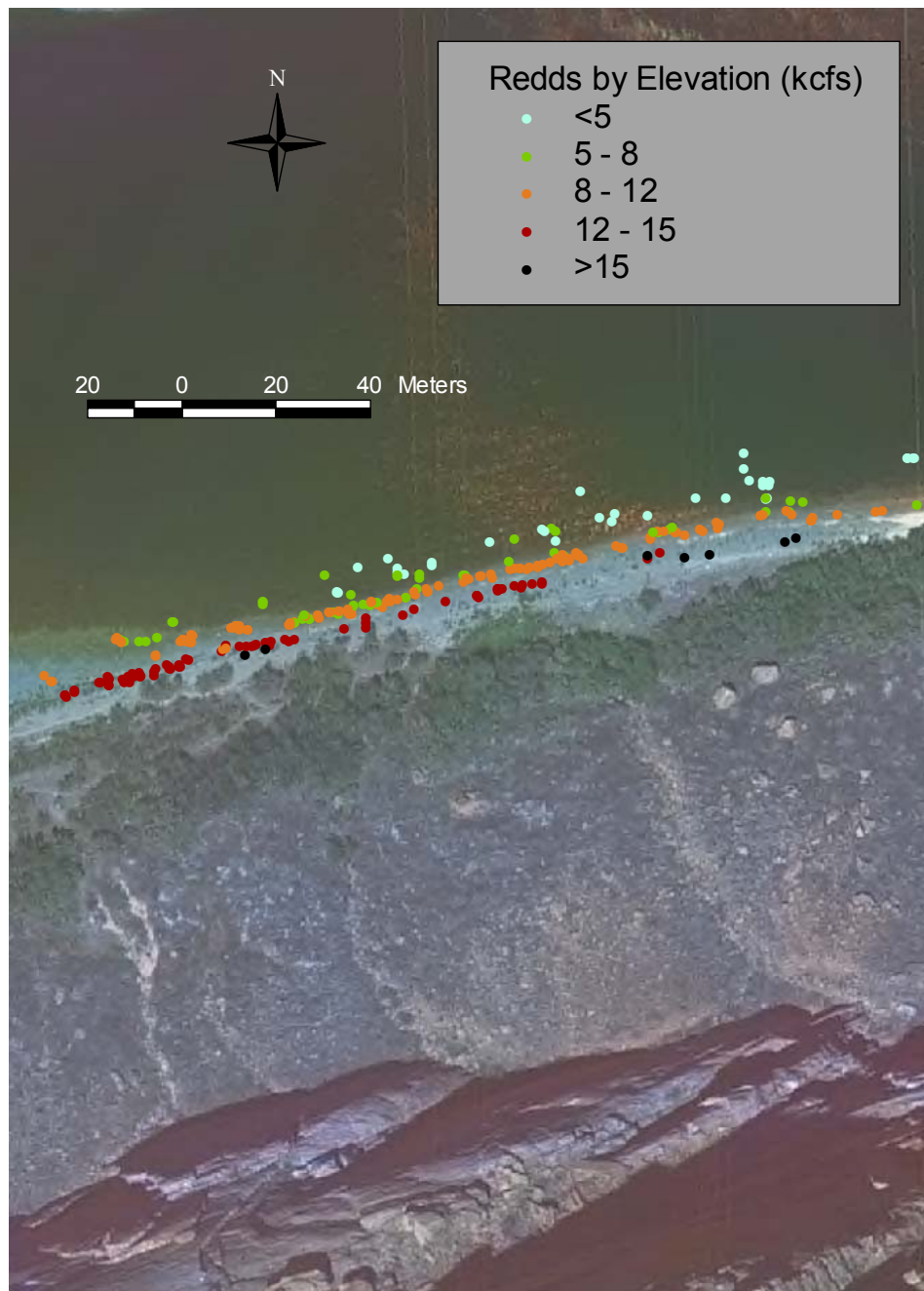


Figure 2.5. Con't.

c) Ferry Swale

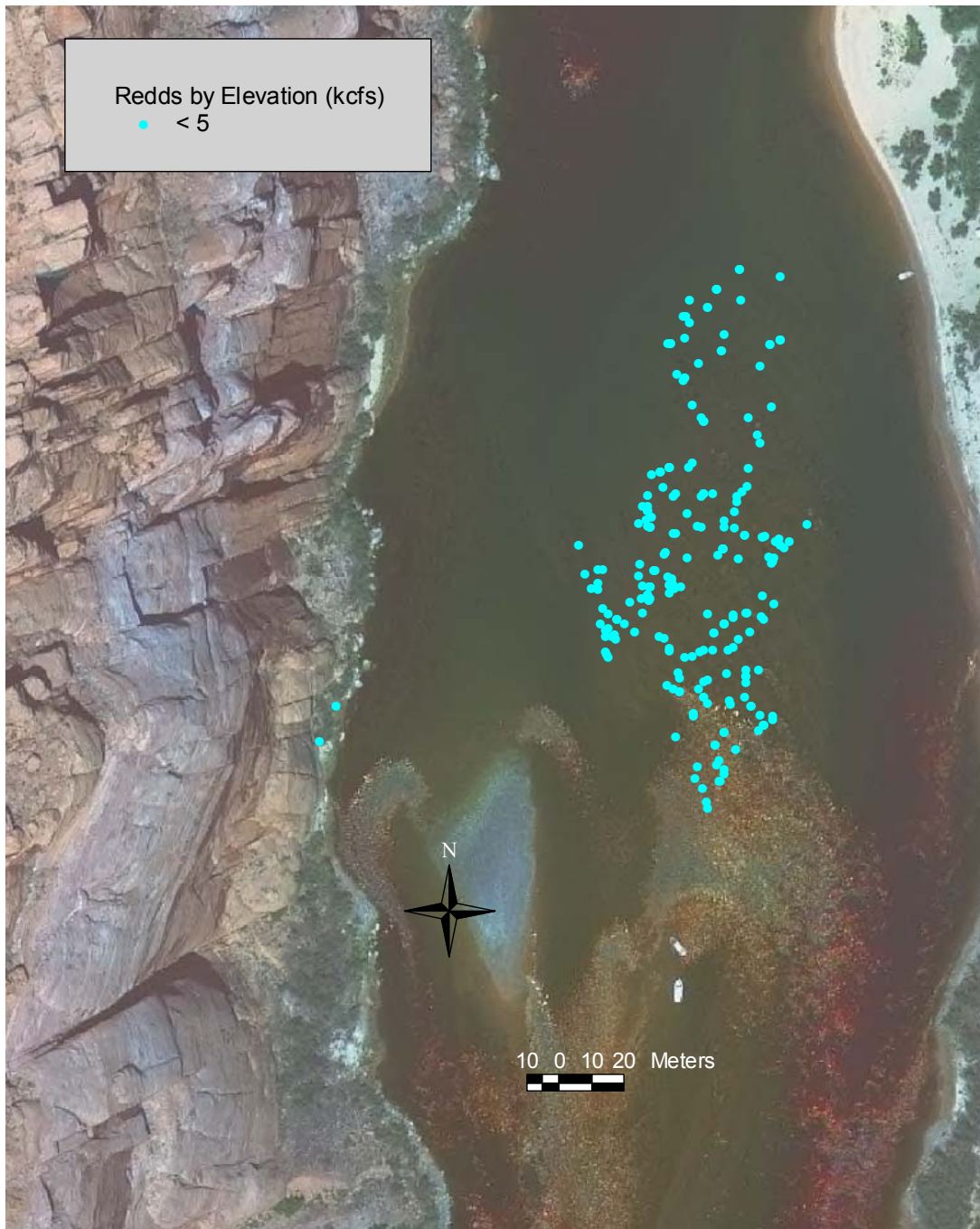


Figure 2.5. Con't

d) Four Mile Bar

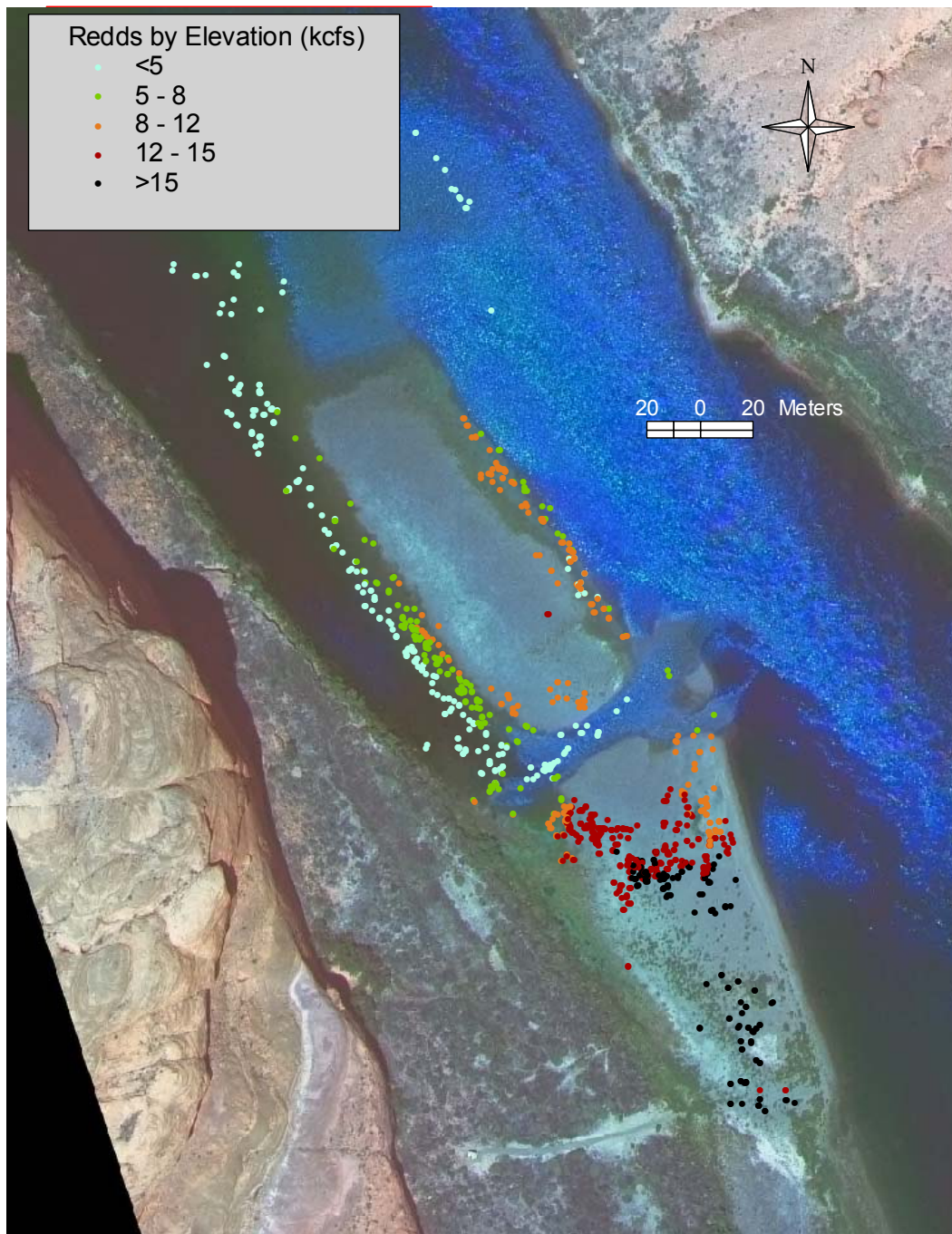


Figure 2.5. Con't.

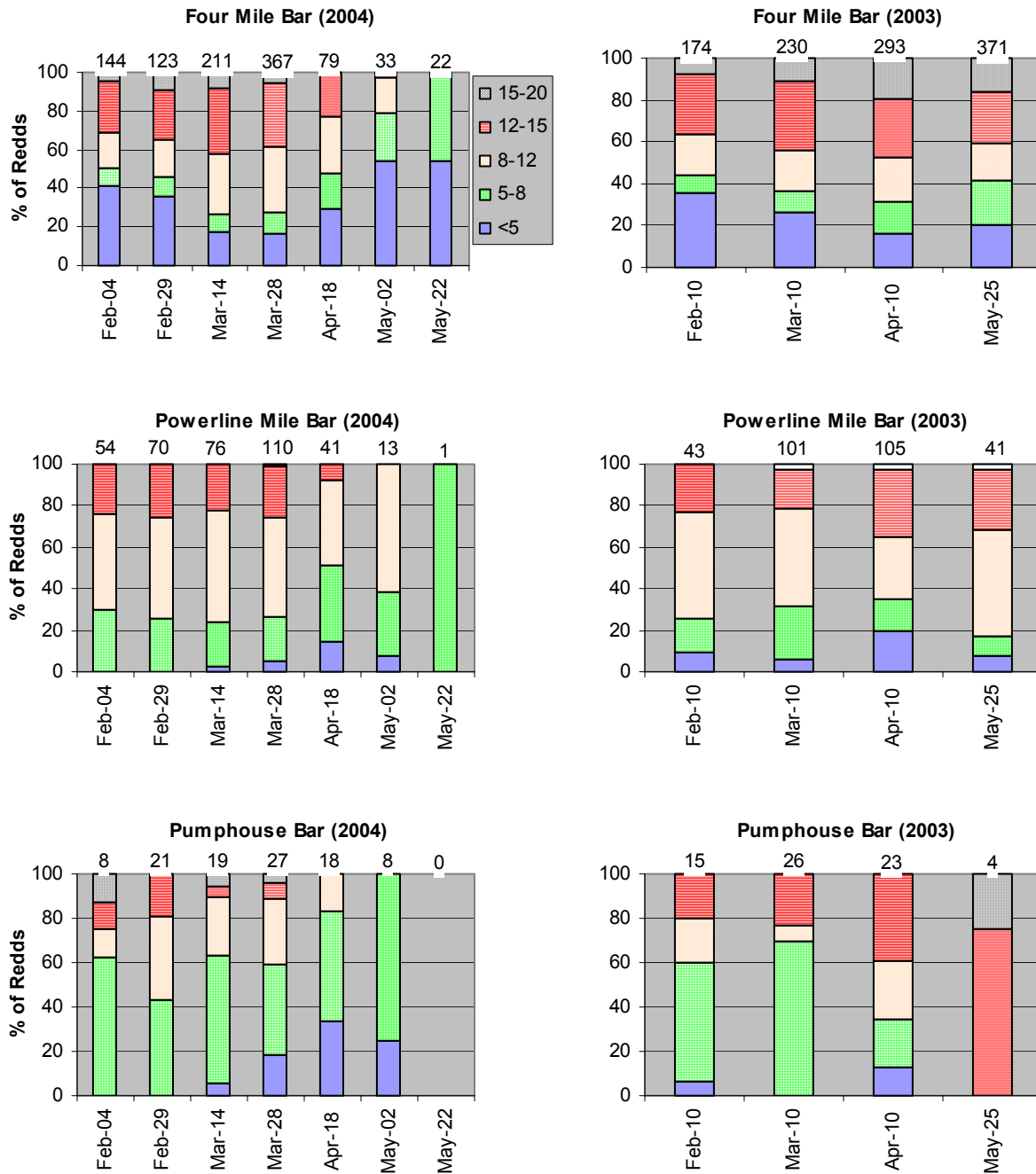


Figure 2.6. Percentage of redds excavated at different elevations (kcfs) across all surveys of high-elevation intensive survey sites in 2003 and 2004. Numbers at the top of the bars indicated the total number of redds counted.

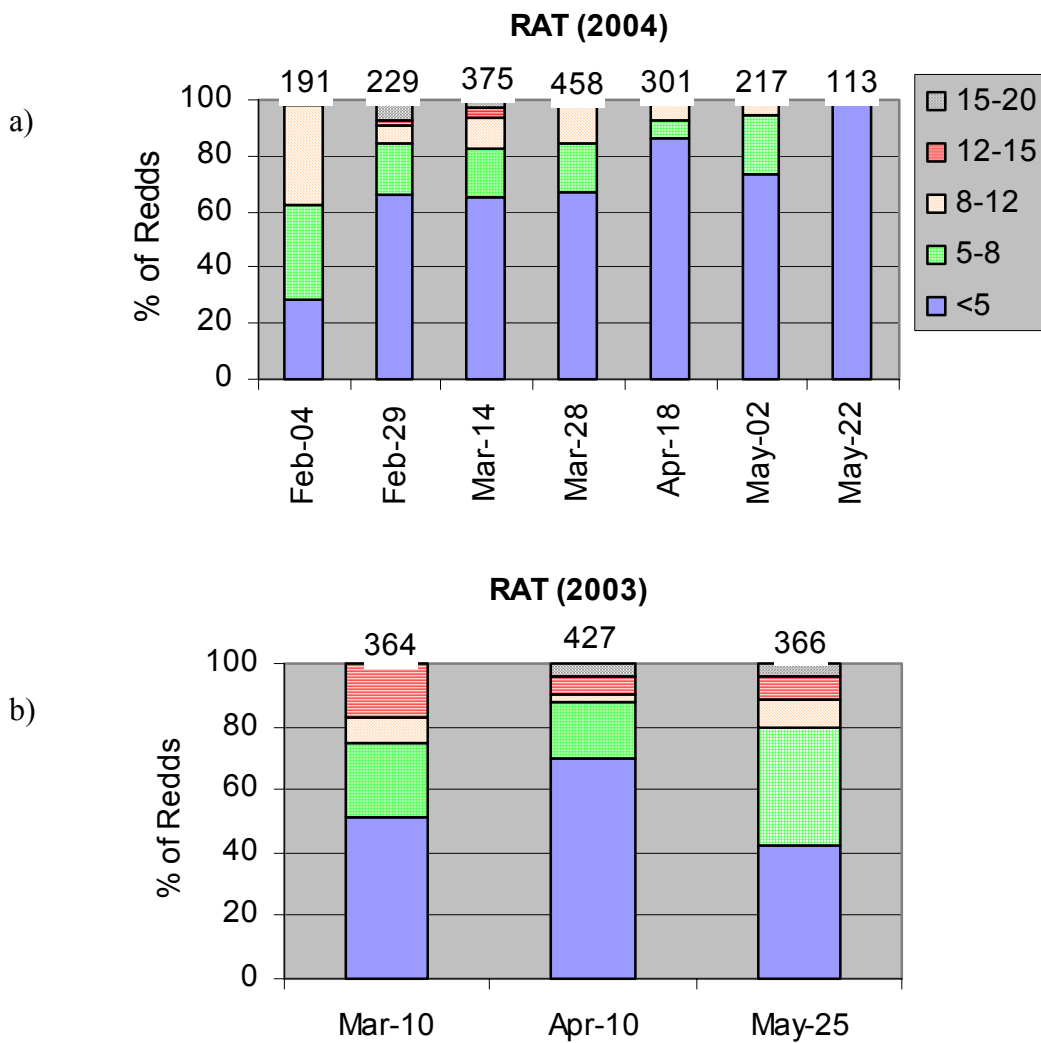


Figure 2.7. Percentage of redds excavated at different elevations (kcfs) across all surveys at rapid assessment (RAT) sites in a) 2004 and b) 2003. Numbers at the top of the bars indicated the total number of redds counted.

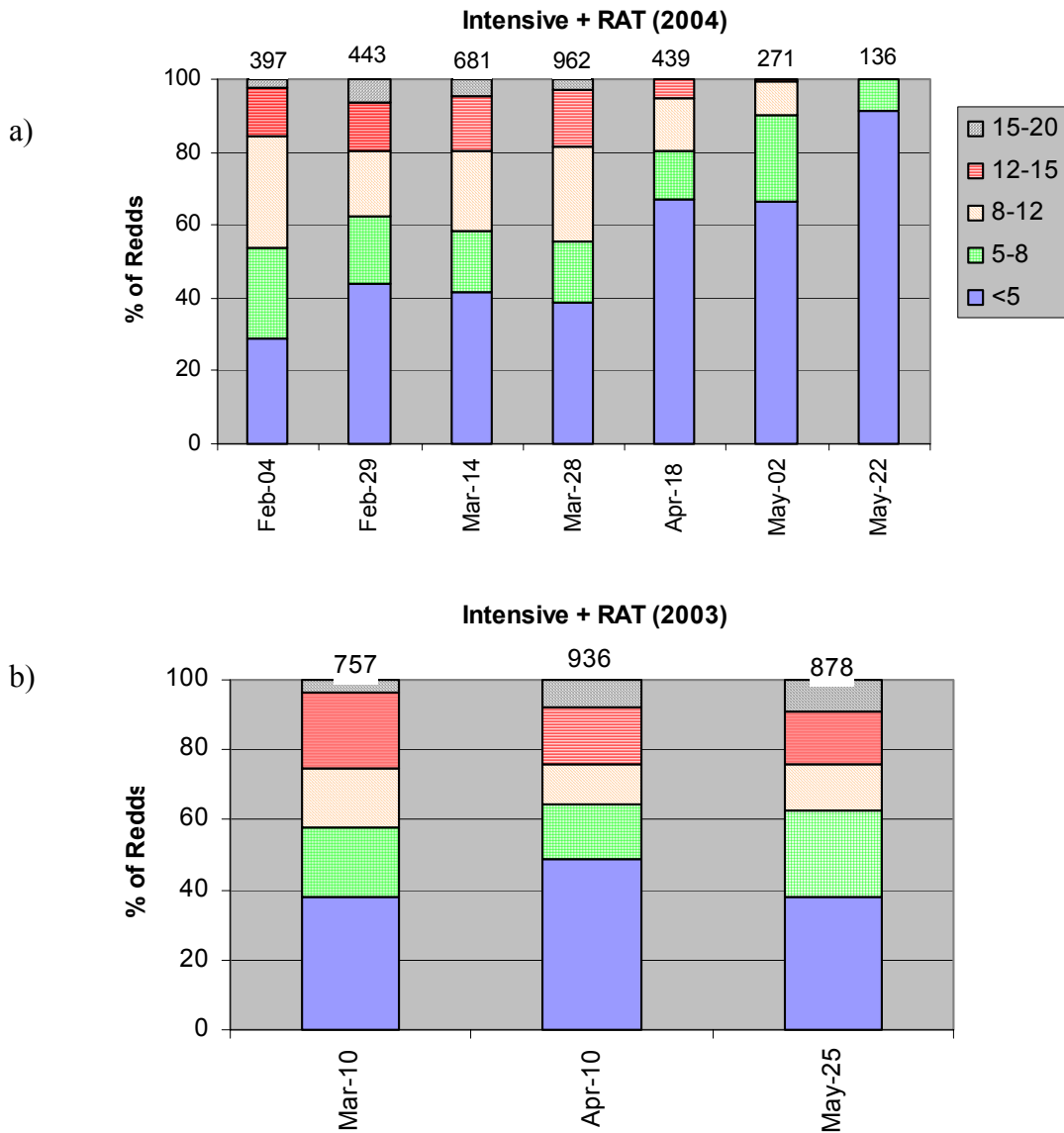


Figure 2.8. Percentage of redds excavated at different elevations (kcfs) across all surveys (intensive + RAT sites combined) in a) 2004 and b) 2003. Numbers at the top of the bars indicated the total number of redds counted.

Table 2.5. Summary of redd counts by site in 2003 and 2004 showing the peak count and elevation (kcfs) where the majority of spawning occurred.

Site Name	River Mile	2003		2004	
		Peak Count	Dominant Elevation	Peak Count	Dominant Elevation
Buoy Island	-15.3	4	8-12	7	5-8
Dam Island (River-Right)	-15	13	12-15	11	8-12
Dam Island (Deep)	-14.9	16	<5	12	<5
PumpHouse	-14.5	26	12-15	27	5-8
14 Mile Bar (River-Right)	-14.4	14	5-8	4	5-8
Powerline Bar	-13.8	105	8-12	110	8-12
Center of Chan. U/S of Honey Draw	-13.4	52	<5	21	<5
Tire Bar	-13.2	19	12-15	37	8-12
Catchings Bar	-12.7	2	<5	1	8-12
Center of channel at U/S end of Slough	-12.4	68	<5	38	<5
Prop Bar at Stranding Pool	-11.8	7	5-8	12	5-8
Long Bar	-11.3			26	8-12/15-20
Ferry Swale	-11.1	96	<5	58	<5
Petroglyph Bar on River-Left	-10.2	4	<5		
Duck Island Main	-10	48	<5	77	<5
Duck Island Inside Chan. at D/S end	-9.9	62	5-8	102	<5
Duck Island Inside Chan. U/S on RR	-10			24	5-8
D/S of Duck Island in Center Channel	-9.3	4	<5	36	5-8
8 Mile Bar	-9	37		5	8-12
7.5 Mile Bar on River-Right	-8.8	4		2	5-8
7.5 Mile Bar on River-Left	-8.2	49	5-8	47	5-8
6 Mile Bar on RL	-5.8	6	5-8	4	5-8
Cliff on River-Right U/S of FM	-4.3	34	<5		
Four Mile Bar	-4.1	372	12-15	367	<5
Water Holes	-3.9	12	5-8	5	5-8
3.5 Mile Bar	-3	98	<5	42	<5
Fall Ck.	-2.5	4	8-12	6	5-8
Total Peak Count Across Sites		1156		1081	

Since flows were dominantly below 12 kcfs after March 31st for the duration of the spawning season, these redds would have been permanently exposed after this date. The majority of these redds, which must have been excavated in February or March were no longer classified as redds during the late-May survey in 2004, but they were in 2003. There is a reasonable amount of subjectivity in determining whether a redd that has been dewatered for a prolonged period of time still has a sufficient number of characteristics to be classified as an active redd. Application of a more stringent classification in 2004 relative to 2003 could explain the discrepancy seen in the fraction of redds above 12 kcfs during latter surveys. We are more confident in our estimate of spawn timing and the total number of redds excavated in 2004 than in 2003 because: a) it was the second year of the study and methodologies were more standardized; b) fewer observers were used in 2004 (3) compared to 2003 (7); and c) surveys were conducted more frequently in 2004 which likely resulted in a more consistent classification. However, there is also evidence from the spatial analysis that there was more spawning late in the year in 2003 compared to 2004 (Table 2.3). For example, the number of ‘new’ redds at Four Mile Bar between April 10 and May 25 in 2003 (212) at elevations below 12 kcfs was double the value in 2004 over a similar time period (March 28 – May 22). Differences in redd counts and hypsometry derived from May surveys in 2003 and 2004 were therefore likely the result of both real changes in spawn timing and inconsistency in redd determinations among years.

Intergravel water temperatures at Four Mile and Powerline Bars increased with elevation and over the duration of the spawning period (Fig. 2.9). At Four Mile Bar, temperatures exceeding a lethal egg incubation limit of 16 C were reached at elevations of 12 kcfs and higher by early- to mid-March in both 2003 and 2004. The weekly pattern in temperatures between January and March in 2004 was caused by Sunday steady flows of 8 kcfs, which exposed elevations above this discharge for the entire daylight period. Lethal temperatures at Powerline Bar in 2004 at elevations of 10 kcfs and higher occurred a few weeks earlier compared to 2003, again, because of the implementation of Sunday steady low flows in 2004. In 2003, flows from GCD were not increased until 9:00 am

between January and March, and the rise in discharge at Four Mile Bar, approximately 11 miles downstream from the dam, did not begin until about 11:00 am (Fig. 2.10). This allowed sufficient time for elevations of 10 kcfs and higher at Four Mile Bar to exceed the maximum temperature limit on a daily basis. This pattern in 2003 was not evident at Powerline Bars (1.5 miles below dam) because flows increased much earlier in the morning before solar radiation and air temperatures had a chance to increase intergravel water temperatures.

Redd elevation data were temporally stratified to determine hypsometry for the redd loss model (Table 2.6). The first system-wide survey conducted in 2003 (RAT + Intensive sites) occurred on March 10th. Consequently, there was no information on redd hypsometry prior to implementation of the experimental regime on January 1st in this year. Data from the first system-wide survey on February 4th in 2004 was therefore used to represent the hypsometry during the November-December period in both 2003 and 2004. Data from the March 10th and April 10th survey in 2003 and the February 28th, March 14th, and March 28th survey in 2004 were used to represent the January-March hypsometry in those years. Data from February 4th survey in 2004 were not used for hypsometry estimates for the January-March model period as they would have been effected by redds that were deposited before January 1st that had not yet exceeded their survey life. Hypsometry values between January-March were very similar among years, however, there was a much higher proportion of redds at higher elevations for the April-June period in 2003 (based on the May 25th survey) compared to 2004 (based on surveys on May 2nd and May 22nd). April surveys were not used in determining hypsometry for the April-June model period as the hypsometry would be biased by redds that were deposited during the experimental flow period but had not yet exceeded their survey life.

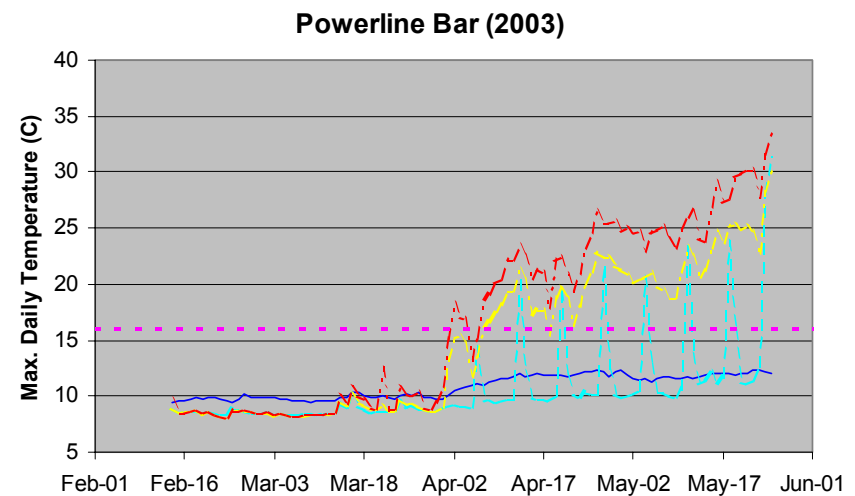
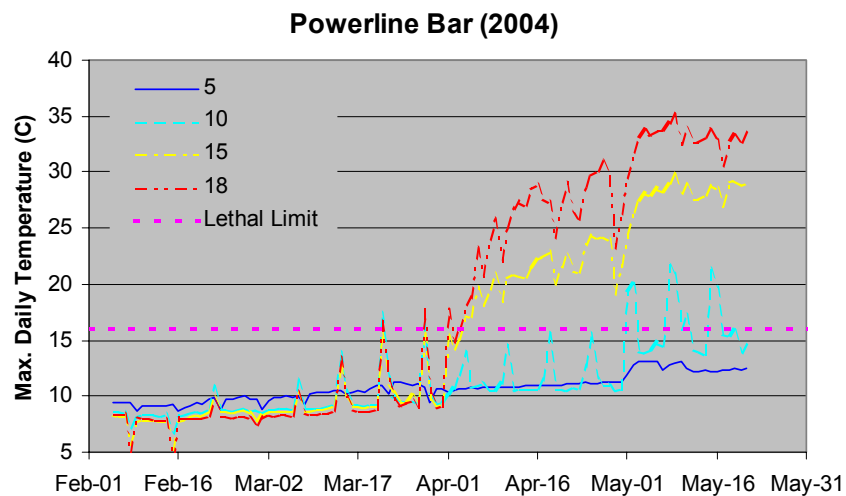
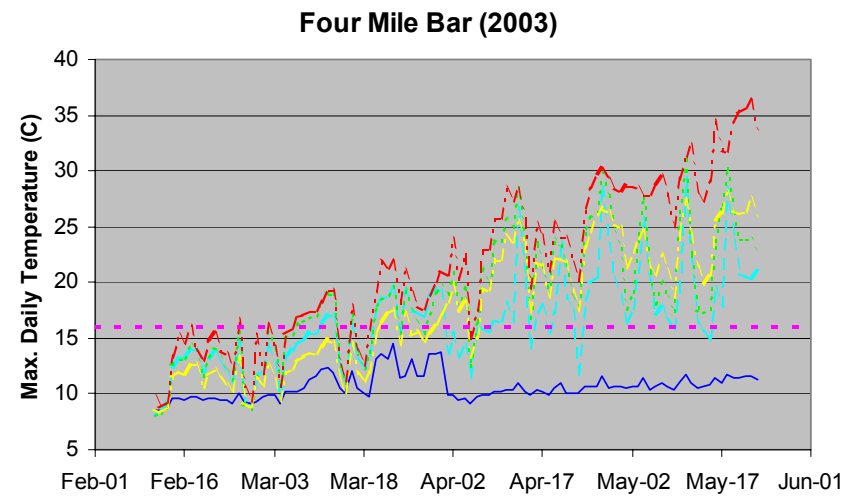
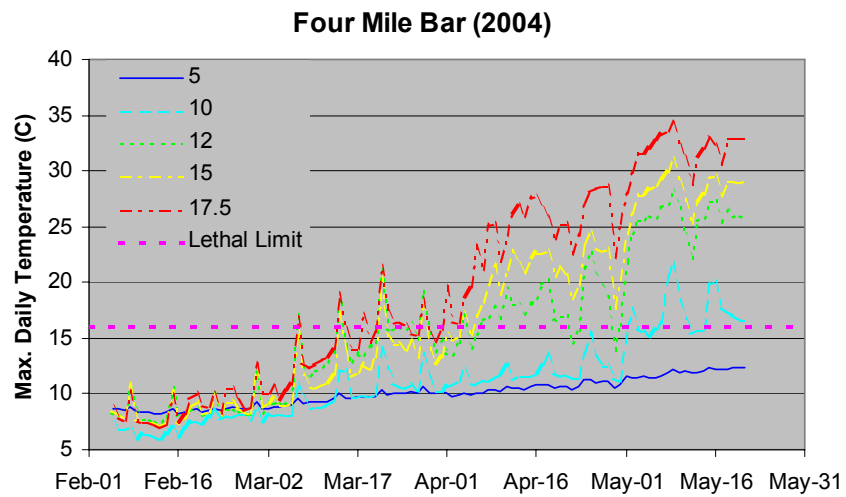


Figure 2.9. Maximum daily intergravel temperatures at Four Mile and Powerline Bars during the winter and spring of 2003 and 2004. A maximum lethal temperature limit of 16 C is shown for reference.

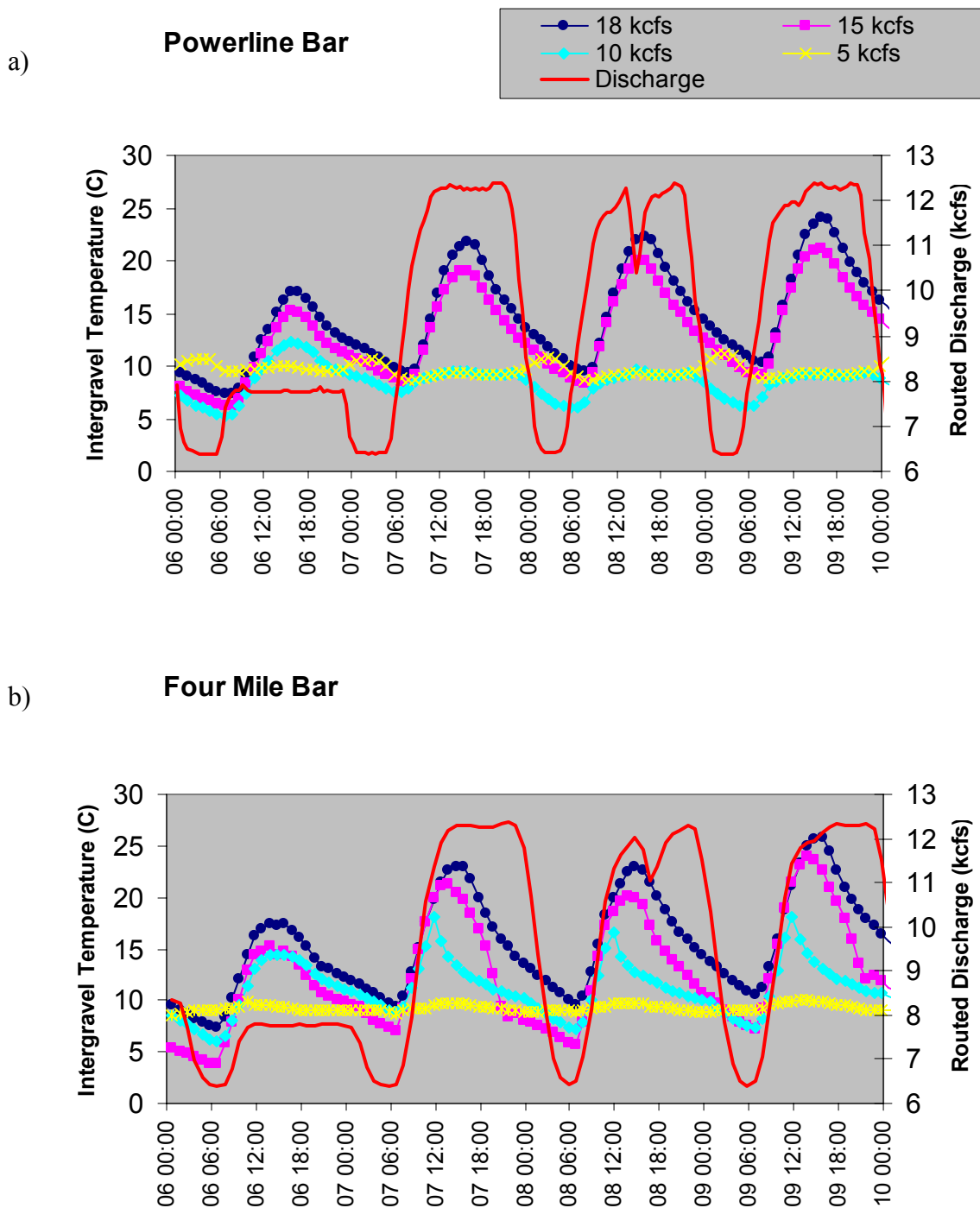


Figure 2.10. Comparison of intergravel thermographs and hydrographs (Apr. 6-9, 2003) at a) Powerline Bar and b) Four Mile Bar.

Table 2.6. Proportion of redds excavated by elevation and month used in the redd loss model.

	Elevation (kcfs)				
	<5	5-8	8-12	12-15	15-20
2004					
Nov-Dec.	0.34	0.30	0.36	0.00	0.00
Jan.-Mar.	0.41	0.17	0.23	0.15	0.04
Apr.-Jun.	0.75	0.19	0.06	0.00	0.00
2003					
Nov-Dec.	Data from Nov-Dec. 2004 used for this period				
Jan.-Mar.	0.44	0.17	0.14	0.19	0.06
Apr.-Jun.	0.46	0.33	0.21	0.00	0.00

Estimates of the percentage of redds that did not produce viable young due to incubation-related mortality at high elevation spawning sites (Four Mile and Powerline Bars) ranged from 45-48% in 2003 and 59-73% in 2004 (Table 2.7). Redd loss in 2004 was higher because of the earlier onset of lethal maximum temperatures due to the implementation of Sunday steady low flows between January and March, and the higher proportion of spawning that occurred during this period in 2004. Estimates of redd loss for the entire reach were 23% in 2003 and 33% in 2004. These estimates were much lower than at the intensive sites because system-wide, there was a much higher fraction of redds excavated at lower elevations. The model predicted that there was no mortality for redds at elevations below 8 kcfs for the reach-wide assessment because temperatures averaged across Four Mile and Powerline Bars never exceeded the lethal incubation limits at elevations below this discharge.

Table 2.7. Model estimates of the % of redds lost by site and elevation (kcfs) as a result of intergravel temperatures exceeding 16 C or dropping below 3 C. FM, PL, and ‘All Sites’ refer to Four Mile Bar, Powerline Bar, and all intensive and RAT sites combined, respectively.

		All Elevations	<5	5-8	8-12	12-15	15-20
FM-2004	Total Redds	570	150	84	153	152	31
	Surviving Redds	233	150	84	0	0	0
	% Lost	59	0	0	100	100	100
FM-2003	Total Redds	1407	401	348	377	183	97
	Surviving Redds	779	401	348	14	16	0
	% Lost	45	0	0	96	91	100
PL-2004	Total Redds	242	9	60	124	48	1
	Surviving Redds	65	9	48	1	7	0
	% Lost	73	0	20	99	86	94
PL-2003	Total Redds	355	53	72	165	58	7
	Surviving Redds	183	53	72	37	20	0
	% Lost	48	0	0	77	65	100
All Sites-2004	Total Redds	2142	1069	374	401	234	65
	Surviving Redds	1443	1069	374	0	0	0
	% Lost	33	0	0	100	100	100
All Sites-2003	Total Redds	4033	1811	1019	716	365	122
	Surviving Redds	3098	1811	1019	151	117	0
	% Lost	23	0	0	79	68	100

Variation in redd loss across elevations was driven by differences in the timing of both lethal intergravel water temperatures and spawning. The model predicted that there was a small loss of redds in December and January in 2004 (Fig. 2.11) due to intergravel temperatures dropping below the 3 C limit. In 2003, the model predicted that virtually all redds excavated before February 20 produced viable young because temperatures exceeding the maximum limit were not reached until later in the year relative to 2004 and

temperatures never dropped below the minimum limit. There was a noticeable decrease in redd loss after March 31st in both years due to a shift to lower spawning elevations resulting from the flow change. Hypsometry data from 2004 suggests that there was virtually no spawning at elevations above 8 kcfs after March 31st, and consequently, the model predicted no redd loss after this date. Redd loss after March 31st was higher in 2003 because there was a higher proportion of redds excavated between 8-12 kcfs.

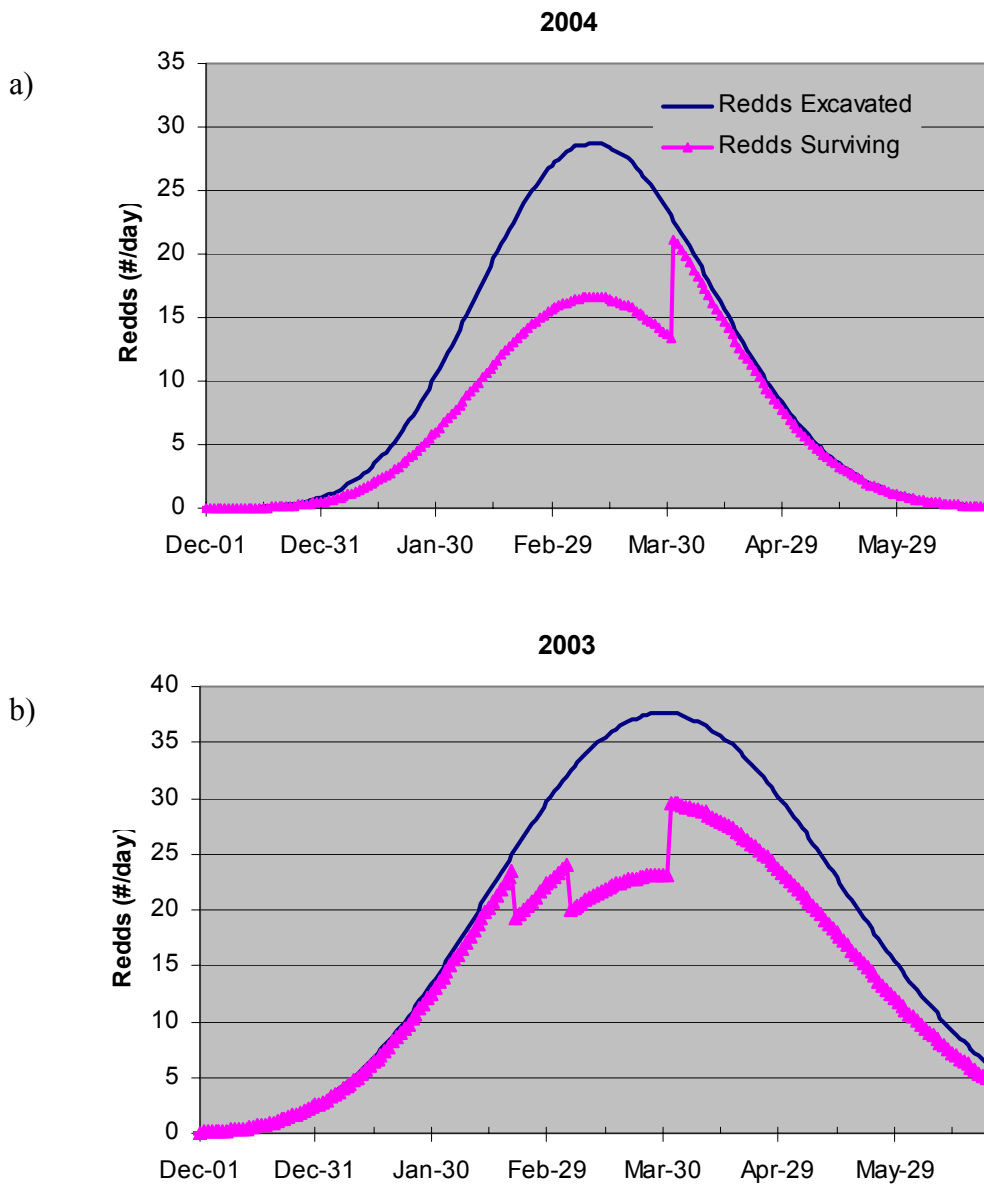


Figure 2.11. Predicted number of redds excavated per day in Glen Canyon and the predicted number that produced viable young (redds surviving) in a) 2004 and b) 2003.

Error in model predictions of redd loss will depend on uncertainty in spawn timing, hypsometry, intergravel temperatures, and predicted mortality as a function of temperature. We have direct field data on the first three of these components and believe the greatest uncertainty in our model is likely associated with the relationship between mortality and temperature. To evaluate the sensitivity of the model to temperature-mortality parameters, we recomputed redd loss estimates using maximum lethal limits of 20 and 18 C and a minimum limit of 0 C. The sensitivity of redd loss estimates to temperature parameters varied by site and year and depended on the thermal history of each case (Table 2.8). For example, Four Mile Bar was insensitive to temperature parameters in 2004 but redd loss in 2003 dropped by 10% when the maximum temperature limit was increased to 20 C. In contrast, redd loss at Powerline Bar was insensitive to temperature limits in 2003 but very sensitive to both maximum and minimum temperature limits in 2004. The reach-wide assessments of redd loss were relatively insensitive to temperature limits in both 2003 and 2004, with the exception of the 20 C maximum limit in 2004, which reduced the redd loss estimate by about 50%.

Table 2.8. Sensitivity analysis showing estimates of the percentage of redds lost under different assumptions about maximum and minimum lethal incubation temperature limits. FM, PL, and All refer to Four Mile Bar, Powerline Bar, and all intensive and RAT sites combined, respectively.

Maximum Limit (C)	20	18	16	16
Minimum Limit (C)	3	3	3	0
FM-2004	57	59	59	56
FM-2003	34	41	45	45
PL-2004	36	46	73	52
PL-2003	46	47	48	48
All-2004	16	29	33	28
All-2003	19	22	23	23

We compared the 2004 redd loss estimate with what would be expected under normal ROD flows as well as from other regimes targeted at increasing incubation mortality. Volumes released from GCD in January, February, and March 2004 were 856,

644, and 644 thousand acre-ft (KAF). Under the higher volume, the Hydro LP operations model predicts a Sunday minimum flow of 12 kcfs and normal daily range of 12-19 kcfs (C. Burbidge, Western Area Power Administration, Salt Lake City, UT, unpublished data). This flow regime would result in only 14% incubation mortality, as all redds below 12 kcfs would likely survive. Under the lower volume of 600 KAF the Sunday steady flow is predicted to be 8 kcfs with a normal daily range of 9-15 kcfs. This flow regime would likely produce a similar mortality to what occurred under the 5-20 kcfs flows in January-March 2004 (33%) assuming that the proportion of redds above 8 kcfs would be similar to what we observed. This assumption is reasonable as the proportion of redds above 15 kcfs was never higher than a few percent (Fig. 2.8). The additional incubation mortality resulting from the enhanced fluctuating flow regime in 2004 would therefore have been 19% in January (i.e., 33% - 14%) and virtually zero in February and March when the majority of spawning occurs. Thus, we conclude that there was virtually no additional mortality associated with the January-March elevated daily flow range relative to what would have occurred normally under ROD operations.

We simulated an extension of enhanced fluctuating flows through the month of April by assuming that redd hypsometry in April would be similar to that from January through March. This action increased the mortality rate from 33% to 40% in 2004 (Table 2.9). We simulated a daytime Sunday steady flow of 5 kcfs between January and March by assuming that intergravel temperatures on Sunday at 5-8 kcfs would be similar to those at 8-12 kcfs in 2004. This scenario increased redd loss from 33% to 49% (Table 2.9). The combined application of the April fluctuating flow extension and a Sunday minimum flow of 5 kcfs increased the redd loss rate to 56%. This last estimate, while almost double the estimate for 2004, is likely well below the incubation losses that occurred prior to the implementation of interim-flows beginning in 1992. Maximum and minimum daily flows from January to May from 1988 to 1991 typically ranged from 15-20 kcfs and 1-3 kcfs, respectively. The maximum daily flows would have likely produced similar hypsometry to what was observed in 2003 and 2004 during the experimental flow period, however this pattern would have been extended over the entire spawning period. The very low daytime flows would have caused much higher incubation mortality. If we

assume that 60% of the redds would have been deposited below 5 kcfs over the entire spawning season (Fig. 2.7) and that more than half of these redds would have been subject to lethal temperatures due to daytime low flows of 1-3 kcfs, the total annual loss of redds from 1988-1991 exceeds 75%. This estimate is at least twice the loss rate that occurs under experimental fluctuations or normal ROD operations.

Table 2.9. Estimates of the percentage of redds lost under different flow regimes from Glen Canyon Dam. See text for a description of regimes.

Scenario	% Redds Lost
2004 (Jan.-Mar. fluctuations, 8 kcfs Sunday min.)	33
2004 ROD (Sunday min = 8-12 kcfs, Max. = 15-19 kcfs)	14-33
Extended Fluctuations through April	40
Sunday Steady Flow of 5 kcfs	49
Extended Fluctuations & Sunday Steady Flow of 5 kcfs	56
Pre Interim/ROD Flows (late 1980s)	ca. >75

We provided a rough verification of trends in egg and alevin mortality by directly examining the viability of embryos in a small fraction of redds. Out of a total of 125 redds that were examined in 2004, 80 contained eggs (Table 2.10). Inferences from redds without eggs are difficult to make and could indicate: that fry had already emerged; complete mortality and decomposition of eggs or alevins had already occurred; failure to find the egg pocket; or the presence of a test pit or ‘false redd’. Limiting the analysis to the 80 redds that contained eggs from which more defensible inferences can be made, 30% showed signs of some and generally complete egg mortality (Fig. 2.12). The percentage of redds with dead eggs increased with elevation and was higher during April-May (78%) than in February-March (24%). We suspect that the actual redd mortality rate later in the year was higher than the data suggests as many of the redds without eggs excavated later in the season had a decomposing fish-like smell which was probably indicative of egg or alevin mortality. In a broad sense, these findings are consistent with our model that predicts increased redd loss at higher elevations and later in the year due to higher intergravel water temperatures.

Table 2.10. Summary of the redd excavation study by elevation (in kcfs) and season.

	Feb-Mar	Apr-May	Total
Redds Examined			
<8	27	8	35
8-12	46	12	58
12-20	32	0	32
Total	105	20	125
Redds with Eggs (Live or Dead)			
<8	15	5	20
8-12	33	4	37
12-20	23		23
Total	71	9	80
% Redds with Dead Eggs			
<8	13	60	25
8-12	24	100	32
12-20	30		30
Total	24	78	30



Figure 2.12. Egg pocket of a redd excavated at Pumphouse bar showing live (clear) and dead (opaque) fertilized eggs.

2.3 Conclusions from Redd Hypsometry and Timing Study

The 2004 total redd loss estimate of 33% was higher than the 2003 estimate of 23%. Differences in redd loss were driven by apparent changes in the timing of spawning and the dates when lethal incubation temperatures first occurred. A higher proportion of spawning occurred between mid-February to late-March in 2004 (60%) compared to 2003 (40%) although part of this difference could be due to changes in survey methodology. Examination of the temporal dynamics of redd loss (Fig. 2.11) showed that redd loss rates were highest for those excavated between February and March because of the combined effects of hypsometry and thermal history. Lethal incubation temperatures

occurred one to two weeks earlier in 2004 (March 21st at 12-15 kcfs, March 28th at elevations > 8 kcfs) compared to 2003 (April 1st at 12-15 kcfs, April 12th at elevations > 8 kcfs). It is likely that implementation of a steady flow of 8 kcfs on Sunday during the January-March experimental flow period in 2004, but not in 2003, was responsible for the differences in the timing of lethal temperatures between years. While the explanation for the inter-annual difference in redd loss rates is helpful in understanding model dynamics, it is quite likely that the difference was smaller than the error of the estimates within a year. It is probably more accurate to state that about 25-30% of the redds excavated in 2003 and 2004 did not produce viable young and that differences among years were within the expected error of the assessment method.

Based on predicted daily flow ranges from the Hydro LP model under normal ROD operations from January to March in 2004, the redd loss model predicted a very similar total mortality relative to what was estimated under the experimental fluctuations. Incubation mortality was mostly determined by the proportion of redds located above the Sunday daytime steady flow elevation. The hypsometry data suggests that, although a greater daily flow range likely increases the proportion of redds at the highest elevations at a few sites that have high elevation spawning habitat, it doesn't likely change the proportion above the Sunday steady flow elevation on a system-wide basis and therefore doesn't provide much incremental mortality relative to the ROD Modified Low Fluctuating Flow (MLFF) operation. This prediction needs to be evaluated in the field by repeating the redd survey under normal ROD operations.

A redd loss rate of 25-30% is likely one-third to one-half the rate experienced in the late-1980s and early-1990s when there was little natural reproduction of rainbow trout in Glen Canyon (Mckinney et al. 1999). Extending enhanced fluctuating flows through April would likely result in a small increase in the total redd loss rate, however more substantial gains in mortality could be achieved by combining this extension with a Sunday daytime minimum flow of 5 kcfs. Our model predicted that this scenario would likely double the extent of incubation mortality compared to what was achieved in 2003 and 2004.

Of all life stages, it is probably easiest to reduce the survival rate of eggs and alevins through changes in flow from Glen Canyon Dam. These stages have no, or very limited mobility, and therefore almost no ability to adjust their position to remain submerged. On the other hand, increased mortality at one life stage could be compensated for by reduced mortality at a later life stage due to reduced densities. The extent of such compensation is uncertain, but it could be large enough to overwhelm any intended effect associated with a non-native flow suppression effort. The older the life stage affected by such flows, the less opportunity for reduced density-dependent mortality at a later life stage. In this sense, targeting incubating life stages is least likely to result in a meaningful reduction in the overall recruitment to the adult population.

It should be stressed that our estimates of redd loss are not based on direct measurements but instead are derived from a simple model supported by extensive field observations. We have reviewed some of the uncertainties in model structure, parameters, and data that could lead to erroneous conclusions about the extent of redd loss and how it varies with dam operations. The only legitimate test of our methodology is to apply it in years with a significantly different flow regime, and compare redd loss estimates with the density of newly emerged fry derived from a young-of-year monthly electrofishing program conducted over the spring and summer (Section 4.0). This test would not validate the absolute estimates of redd loss but would be a good test of the methods' ability to capture relative changes in redd loss due to dam operations.

3.0 Spawning Habitat Preference

Increased experimental flow fluctuations from Glen Canyon Dam implemented in January through March of 2003 and 2004 were in part designed to increase the elevations where rainbow trout would spawn. In theory, higher maximum discharges would lead to increased depth and velocities and shift preferred spawning habitat to higher elevations where daily exposure periods would be longer. A proportion of redds deposited at the highest elevations would be completely dewatered following a reduction in the maximum discharge after March 31st. Partial or permanent exposure of redds would lead to increased or complete mortality of incubating life stages and potentially reduce the population size of rainbow trout in Grand Canyon.

Physical characteristics of salmonid spawning habitat have been well documented. In Montgomery and Tinning's (1993) review of rainbow trout spawning habitat characteristics, average water velocities and depths ranged from 0.3-1.0 m/sec and 0.3-0.8 m, respectively. There are no estimates of velocity and depth preferences for rainbow trout spawning in Glen or Grand Canyon, however a number of studies have examined gravel characteristics in spawning habitat. Kondolf et al. (1989) reported a median grain size (D50) for redds located below Glen Canyon Dam (Four- and Eight-Mile Bars) of 10 mm based on pit samples dug to a depth of 15 cm. The average D50 from four spawning areas in Glen Canyon measured on the bar surface by Angradi et al. (1992) was 46 mm, with spawning sites closest to the dam having coarser material relative to sites located downstream. Site morphology has also been shown to play an important role in determining spawning habitat preference. Many salmonid species have been observed to preferentially spawn where stream water down-wells into the gravel bed. Spawning is often observed at the downstream end of pools (tail-outs) where the lower water surface elevation of the downstream riffle creates a hydraulic gradient that induces down welling (Kondolf 2000).

Habitat preference is usually computed as the ratio of the relative utilization of a particular habitat characteristic (e.g. proportion of total redds at depths 0.2-0.4m) to the relative total availability of that condition (Bovee 1982). Values for particular conditions that are larger than one indicate preferential use of that condition, while values less than one indicate avoidance. Preference curves are often used in conjunction with discharge-driven predictions of depth and velocity to compute Weighted Useable Area (WUA). WUA is simply the product of the preference for a particular characteristic and the area of that characteristic. In a two-dimensional application, an area is divided into a series of grid cells, and the sum of the product of the area of these cells and their preferences determines the total WUA at-a-site. Predictions of changes in depth and velocity as a function of discharge are used to evaluate how habitat availability changes in response to flow.

In this section of the report we present results that document rainbow trout spawning habitat preference for depth, velocity, and grain size of the bed surface in Glen Canyon. We conducted intensive surveys of substrate characteristics and of depths and velocities across a range of discharges. Interpolated spatial fields of habitat characteristics developed from these data were used in conjunction with site-specific spawning preference relationships to predict how spawning habitat availability would change as a function of discharge from Glen Canyon Dam.

3.1 Methods for Spawning Habitat Preference Study

3.1.1 Methods for Spawning Habitat Preference Data Collection

We measured depth, water velocity, and grain size at Four Mile Bar, Ferry Swale, and Powerline and Pumphouse Bars in 2003 (Fig. 2.1) across an evenly-spaced grid, and over all redds that were identified during the redd surveys. The locations of all habitat measurements were surveyed with an electronic total station equipped with a digital data collector (see Section 2.1.1 for additional details concerning survey methods and

accuracy). Measurements of depth and velocity were taken at steady flows of 5, 8, 12, and 20 kcfs. Measurements in shallow areas were made by wading with a Swoffer current meter attached to a topset wading rod. Velocities were taken at $6/10^{\text{th}}$ of the total depth and 8 cm off the bottom. For areas that could not be waded, velocities were measured by lowering the impeller of the current meter to $2/10^{\text{th}}$ and $8/10^{\text{th}}$ of the total depth using a $3/4''$ steel pipe mounted to a sliding attachment at the bow of a 7m aluminum-hulled motorized boat. It was not always possible to lower the impeller to $8/10^{\text{th}}$ of the total depth when water velocities or depths were high. In these cases, the depth of the measurement was usually 1.5 m. The depth of each velocity measurement was always recorded. Total depth was measured with a Lowrance depth-sounder.

Grain size of the bed surface was characterized using a modified Wolman pebble count (Wolman 1954). On exposed areas of the bars, a 40-m transect was equally divided into eight 5-m sections. The b-axis for each particle located immediately below the tape at 0.5 m increments was used to classify the particle into one of 18 categories of a modified Wentworth scale (Table 3.1). The starting and ending points of the transect were surveyed and interpolation was used to compute the spatial coordinates at the center of each 5-m section. A 1-m^2 wooden square, equally divided into 81 0.1-m increments, was used to select particles in areas that were not sampled by the transect method. An underwater video camera was used to measure grain size for areas that were submerged at the time of the survey. The video camera was equipped with a topside daylight viewing screen and digital video recording device. Two parallel lasers, located 10 cm apart on top of the camera, provided a horizontal scale for images of the bottom. A short video segment (5-10 sec.) was recorded at each location when the laser points became visible on the substrate. A microphone was used to record a location identifier on the audio track of the videotape. Following the field survey, digital video was downloaded onto a computer in an AVI-format using commercially available digital video editing software. These files were then loaded into a custom-software application (BVIS) to capture a single still image from the video segment for each measurement location (BVIS can be downloaded at <http://www.mountainsoft.net>). The user identified the laser points on the still image so that the scale of the image could be determined. A transect that intersected

the laser points was then automatically drawn across the entire width of the image and divided into 15 equal widths. The b-axis of each particle located at the intersection of the transect and width boundaries was measured by the user and automatically recorded by the software. By measuring particles along an axis where the scale is known, the width of the particles in pixels could be translated into an absolute unit of measurement (mm).

Table 3.1. Particle size categories (b-axis diameter) used to characterize the grain size of gravel bars in Glen Canyon in 2003.

Size Category (mm)	Substrate Type
<2	Sand and Finer
2-24	Small Gravel
24-48	Medium Gravel
48-64	Large Gravel
64-128	Small Cobble
>128	Larger Cobble and Boulder

A bulk sediment sample at Four Mile Bar was obtained by removing approximately 50 kg of sediment from pits dug to 15 cm depth at two locations. In the laboratory, the two samples were split into a total of 48 parts and the mass of sediment in each Phi Class was determined using standard methods (Kellerhals and Bray 1971). A single grain size distribution was derived by combining data across all samples and sub-samples. Note that the grain size distribution from the pit sample was based on the mass of sediment retained in each Phi class, while the distribution for the surface samples was based on the number of particles in each class. Rice and Church (1996) have shown that two grain size distributions may be compared statistically for coarse riverbed sediments.

3.1.2 Methods for Analysis of Spawning Habitat Preference Data

Six statistical descriptors were used to characterize particle size on the bed. D15, D50, and D85 refer to the sizes for which 15%, 50%, and 85% of the sample is finer. The geometric mean (DG), the geometric sorting index (SG), and skewness (SK) were computed using the following formulas provided by Kondolf et al. (1989),

$$(3.1) \quad DG = \sqrt{D15 * D85} ,$$

$$(3.2) \quad SG = \sqrt{\frac{D85}{D15}} ,$$

$$(3.3) \quad SK = \frac{\log(\frac{DG}{D50})}{\log(SG)} ,$$

Computation of grain size statistics at each habitat measurement location were based on a minimum of 10 measurements for terrestrial surveys and 15 measurements for video surveys of submerged substrate.

Water velocity at specific depths at each measurement location was estimated by assuming a logarithmic vertical velocity profile (Gordon et al. 1994). The slope of the log depth-velocity relationship for each location was computed based on velocity measurements taken at two depths. The average water column velocity at 60% of the total depth, and the velocity 10 cm off the bottom were then computed. The latter estimate provided an index of the velocity that a fish would encounter when excavating a redd. The slope (b) of log depth-velocity profile was also used to compute shear stress (τ , in units of $N \cdot m^{-1} \cdot s^{-2}$) from,

$$(3.4) \quad \tau = \rho \times (b / 5.75)^2 ,$$

where, ρ is the density of water (998 kg/cm³ at 20 C). With this formulation, critical shear stress is directly proportional to substrate size. For example, a shear stress of 23 Nm⁻¹s⁻² would be expected to move a substrate particle 23 cm in diameter. The vulnerability of bed movement could therefore be assessed by comparing shear stress with statistics quantifying particle size on the bed (Leopold 1994).

At each survey site, spatial grids of water depth and bottom velocity at specific discharges, and substrate characteristics (e.g., D50), were interpolated from point values using a Universal (linear drift) Kriging algorithm (M. Boeringa, Amsterdam Water Supply, Amsterdam, the Netherlands, unpublished data). A summary of the input data used for these interpolations is provided in Table 3.2. Grid size for the modeled areas at each site was determined based on computational constraints and was 2 m², 1 m², and 1.5 m² for Four Mile Bar, Ferry Swale, and Powerline Bar, respectively. Pumphouse Bar was excluded from the analysis because there were not enough redds to define habitat preference with any degree of certainty (Fig. 2.5a).

A variety of spatial interpolation routines, including alternate Kriging algorithms (quadratic drift, linear and gaussian) and regularized and tensioned splines were assessed using a cross-validation procedure. Surfaces were interpolated using a random selection of 90% of the data for each of the algorithms being assessed. The remaining 10% of the sample points were then compared to the predicted values to estimate accuracy. Ten random draws were performed from topographic and velocity data at Four Mile Bar. Universal Kriging (linear drift) was the most accurate interpolation algorithm in all cases. The accuracy of interpolated topography and velocity measurements was +/- 5 cm and +/- 4 cm/sec, respectively. Portions of interpolated surfaces of depth and velocity located above the water elevation at the time of the survey, an artifact of the interpolation procedure, were removed by overlaying polygons that defined the water's edge. These polygons were digitized from surveyed points along the water's edge at each site at the four discharge levels. All interpolated surfaces above the water's edge for each discharge were removed.

Table 3.2. Number of elevation, substrate, depth, and velocity observations (Points) collected at Four Mile Bar (FM), Ferry Swale (FS), Powerline Bar (PL), and Pumphouse Bar (PH). Depth and velocity observations were collected at 5, 8, 12, and 20 kcfs. The total area of each study site by discharge is also shown (Area m²).

Site	Observation Type	Elevation	Substrate	Depth and Velocity			
				5 kcfs	8 kcfs	12 kcfs	20 kcfs
FM	Points	1868	196	187	348	246	460
	Area (m ²)			12,966	16,864	21,948	28,352
FS	Points	679	136	177	232	141	129
	Area (m ²)			17,818	20,160	21,241	21,328
PL	Points	734	64	52	124	93	257
	Area (m ²)			7,831	8,790	9,705	11,510
PH	Points	335	22	90	79	46	66
	Area (m ²)				Not Computed		
Grand Total Points		3616	418	506	783	526	912

The discharge at which redds were formed needed to be determined for each site to determine habitat preference. Only redd locations from the March survey were selected for the analysis because the redd-forming discharge could be better determined relative to later surveys. The vast majority of redds present during the March survey would have been created at either 5 or 20 kcfs as increased ramping rates during the January to March 2003 experimental flow period limited the amount of time at intermediate discharges. Less than 25% of the redds at Four Mile Bar were located at or below 5 kcfs in March (Fig. 2.6) so the other 75% of the redds must have been created at 20 kcfs. At 5 kcfs, submerged redds tended to be in water less than 10 cm deep and we observed no spawning activity at this flow during any of our surveys. Thus, redds located at or below 5 kcfs were very likely created at 20 kcfs as well. At Powerline Bar only a small fraction of redds were located at or below 5 kcfs so it is reasonable to assume that the dominant

redd-forming discharge was also 20 kcfs. At Ferry Swale we only observed spawning activity at 5 kcfs during February and March surveys. Fish were likely not able to maintain positions over most redds at 20 kcfs due to excessive velocities. Redds created at Ferry Swale prior to April 1st were therefore likely formed at 5 kcfs.

A linear discriminant function analysis (DFA) was used to determine which habitat variables best classified grid cells into “redd” or “non-redd” groups (Systat 1997). All “redd” cells, and an approximately equal number of “non-redd” cells, selected at random across the entire site area, were used as input to the DFA. Utilization, availability, and preference were computed for the three most important variables identified in the DFA. The number of “redd” and “non-redd” cells among 16 depth (0 – 3 m in 0.2 increments), 10 bottom velocity (0 – 1.8 m/sec in 0.2 increments), and 15 D85 categories (0 – 70 mm in 10 mm increments) were computed for each site at its “redd-forming” discharge. Spawning utilization ($U_{c,i}$) for each variable type ‘c’ and increment ‘i’ was computed as the ratio of the number of cells with redds at that increment relative to the total number of cells with redds. Total availability ($A_{c,i}$) was computed as the ratio of the total number of cells at that increment relative to the total number of wetted cells in the site. Plots of utilization and availability as a function of the increment value showed continuous relationships with some scatter likely due to small sample sizes for some increments. Utilization and availability relationships were therefore smoothed by fitting a Beta distribution to the data,

$$(3.5) \quad X_{c,i} = YMax \int_0^i \theta_i^{(\alpha-1)} (1 - \theta_i)^{(\beta-1)} di,$$

where $X_{c,i}$ refers to utilization or availability, α and β are parameters of the Beta distribution that define its shape, θ_i represents the proportional value of the habitat variable that ranges from 0 to 1, and $Ymax$ is a scalar. Note that eqn. 3.5 returns the cumulative frequency, thus point densities for utilization and availability for increment ‘i’ were calculated as the difference between adjacent increments (e.g., $X_{c,i} - X_{c,i-1}$). The

model was fit to the data by minimizing the sum of squared differences between predictions and observed ratios using a non-linear iterative search procedure.

Spawning habitat preference ($P_{c,i}$) was computed as the ratio of smoothed values of utilization and availability,

$$(3.6) \quad P_{c,i} = \frac{U_{c,i}}{A_{c,i}},$$

Spawning preference values larger than one indicated preferential use of that condition while values less than one indicated avoidance. Linear interpolation was used to predict preference for any continuous depth (D), velocity (V), or D85 value associated with a particular grid cell. Habitat values for each grid cells at specific discharges were derived from the interpolated surfaces of depth, velocity, and D85. The overall spawning preference for each grid cell at a specific discharge was computed as the product of the three variable-specific preferences,

$$(3.7) \quad P = P_D * P_V * P_{D85},$$

Weighted useable area at specific discharges was computed as the product of the sum of the product of the overall preference values for all grid cells and the cell area. Note that the overall preference model assumes that each habitat component acts independently on the overall preference and that there are no interactions among variables. However, the model does not assume that all habitat variables are equally important as variables that show little preference would have values close to one.

3.2 Results from Spawning Habitat Preference Study

Redds at intensively monitored sites were generally restricted to the upstream portions of the bars in areas which can be characterized as pool tail-outs or inside river

bends (Fig. 2.5). Chinook and other species of salmon have been observed to spawn where stream water down wells into the gravel bed, which often occurs in pool tail-outs, the upstream ends of debris fans, or inside river bends where the hydraulic gradient is largest (Kondolf 2000). At Four Mile Bar, where there is significant transverse flow from river-right to river-left, the area of maximum hydraulic gradient is likely on river-right, which coincides with the location of the majority of redds.

Grain size statistics for the streambed varied across the three sampling sites (Table 3.3). The median grain size (D50) and presence of larger particles (D85) was lower at Ferry Swale compared to the other sites. Powerline Bar had a higher fraction of smaller particles (D15). Grain sizes at Four Mile Bar and Ferry Swale were generally well sorted (low values of SG), but this was not the case at Powerline Bar. All sites showed a negative skew to the particle size distributions indicative of a longer tail extending into finer sediment sizes. Negative skew is a common characteristic of stream gravels used by spawning salmonids (Kondolf et al. 1989). D16, D50, and D86 values reported by Kondolf et al. (1989) for Four Mile and Twelve Mile Bars were 1, 10, and 30 mm, respectively, and were considerably finer than the statistics at Four Mile Bar in 2003. This difference likely occurred because Kondolf et al.'s statistics were based on substrates collected from pit samples dug to 10-15 cm depth, while the statistics presented in Table 3.3 were based on surface samples only. D15, D50, and D85 statistics from the two 0-15 cm pit samples from Four Mile Bar taken in 2003 were < 2 mm, 10 mm, and 25 mm, respectively. Particle sizes from the pit samples were considerably finer than the surface samples at Four Mile Bar (Table 3.3) because finer material is winnowed from the bed surface. The grain size distribution from the pit samples in 2003 was similar to the distribution reported by Kondolf et al. (1989), but the sample size from both studies is obviously inadequate to determine that surficial grain size has not changed in Glen Canyon since the late 1980s.

Surficial grain size statistics defining particle size (D15, D50, D85, DG) were reasonably well correlated with each other (Table 3.4). Statistics reflecting the shape of the grain size distribution (SG and SK) were not correlated with the other metrics or each

other. Correlations among particle size statistics were highest at Four Mile Bar and Ferry Swale where variance in particle size (SG) was low relative to Powerline Bar.

Table 3.3. Grain size characteristics of substrate taken from the bar surface at Four Mile Bar (FM), Ferry Swale (FS), Powerline Bar (PL), and Pumphouse Bar (PH). N refers to the number of transect locations where statistics were computed, with each location consisting of 10-15 measurements. D15, D50, and D85 refer to the grain size where 15%, 50%, and 85% of the sample is finer.

Statistic	FM	FS	PL
N	196	136	64
Average D15	7.45	6.13	4.96
Average D50	18.67	12.53	19.10
Average D85	36.83	21.05	46.56
Average Geometric Mean (DG)	15.52	10.46	13.41
Average Geometric Standard Deviation (SG)	2.55	2.58	4.73
Average Skewness (SK)	-0.16	-0.18	-0.23

Discriminant functions predicted the presence of redds in grid cells based on habitat characteristics with an accuracy of 76-84% (Table 3.5). The functions explained 59%, 62%, 46%, and 45% of the variance between “redd” and “non-redd” cells for Powerline Bar, Ferry Swale, Four Mile Bar, and all sites combined, respectively. Accuracy was highest at Powerline Bar (84%) and Ferry Swale (79%) and lowest at Four Mile Bar (76%) and for all sites combined (73%). More than half the sample size of the all sites combined analysis was made up of cells from Four Mile Bar. As a result, the pattern at Four Mile Bar dominated the overall pattern. The models tended to predict more false-positives (cells without a redd incorrectly predicted as having one) than false-negatives (cells with a redd incorrectly predicted as not having one). This pattern could reflect error in model formulation or structure, such as not accounting for interactions among variables or failure to include variables that are important components of spawning habitat preference. An alternate explanation for the large number of false-positives is that there were not a sufficient number of spawners to fully utilize the available habitat. Depth, bottom velocity, and D85 were the most important variables for

discriminating among “redd” and “non-redd” cells at Powerline Bar and Ferry Swale. Depth and D85 were the most important variables at Four Mile Bar and when all sites were combined. Water depth, bottom velocity, and D85 were selected as the variables to use for habitat preference and WUA computations.

Patterns in total habitat availability varied considerably by site, however, utilization patterns were reasonably consistent. At Four Mile Bar, depths ranging from 0.5-1.25 m were utilized at a rate considerably higher than their overall availability (Fig. 3.1a). Differences between utilization and availability were much subtler with respect to near-bottom velocity and D85. Depths of 0.75-1.25 m were utilized disproportionately relative to their availability at Ferry Swale and there was also strong preferential use of near-bottom velocities ranging from 0.6-0.8 m/sec (Fig. 3.1b). There also appeared to be preferential use of substrates with D85 values of 20-30 mm. Increased utilization at depths of 0.6 m and 1.2 m was apparent at Powerline Bar (Fig. 3.1c). This is the only case where a bi-modal response in habitat preference was observed and where the Beta distribution failed to capture the habitat relationship. We had to manually alter the Beta distribution for the Powerline Bar depth-utilization curve to provide the fit presented in Fig. 3.1c. At Powerline Bar, we also observed increased utilization at near-bottom velocities of 0.4-0.6 m/sec and for D85s of 20-35 mm.

Spawning habitat preference was somewhat consistent across sites but differences were apparent (Fig. 3.2). In general, depths of 0.5-1.25 m were preferentially utilized (preference > 1). A wider range in preferred near-bottom velocities was observed at Four Mile Bar (0.2 – 0.75 m/sec) relative to Powerline Bar (0.3 – 0.7 m/sec) and there was a preference for higher velocities at Ferry Swale (0.5-1.2 m/sec). Preferential use of particle sizes ranged from 20-30 mm at Ferry Swale to 10-40 mm at Powerline Bar. There was little evidence of preferential use of substrate at Four Mile Bar with the

Table 3.4. Correlations (r^2) among grain size statistics (surface only) at 3 locations in Glen Canyon. D15, D50, and D85 refer to the grain size where 15%, 50%, and 85% of the sample is finer, respectively. DG, SG, and SK, refer to the geometric mean, geometric standard deviation (sorting index), and skewness, respectively.

All Sites						
	D15	D50	D85	DG	SG	
D50	0.38					
D85	0.18	0.61				
DG	0.78	0.62	0.59			
SG	0.25	0.01	0.06	0.09		
SK	0.05	0.07	0.00	0.04	0.12	
Four Mile Bar						
	D15	D50	D85	DG	SG	
D50	0.35					
D85	0.24	0.70				
DG	0.81	0.61	0.64			
SG	0.18	0.04	0.10	0.04		
SK	0.08	0.08	0.00	0.05	0.12	
Ferry Swale						
	D15	D50	D85	DG	SG	
D50	0.59					
D85	0.32	0.74				
DG	0.86	0.76	0.65			
SG	0.28	0.00	0.01	0.15		
SK	0.03	0.04	0.00	0.02	0.11	
Powerline Bar						
	D15	D50	D85	DG	SG	
D50	0.26					
D85	0.13	0.33				
DG	0.77	0.41	0.54			
SG	0.52	0.01	0.00	0.30		
SK	0.11	0.16	0.01	0.09	0.16	

Table 3.5. Summary statistics and classification tables from the discriminant function analysis predicting the presence of redds within grid cells based on the habitat characteristics of depth, near-bottom velocity, and particle size. The larger the F-to-Remove statistic, the greater the relative importance of variables included in the discriminant function.

Powerline Bar							
Canonical correlation		0.59	Predicted				
F-to-Remove			Non-Redd	Redd	Total		
Depth	62		Non-Redd	72	23	95	
Vel	6.0		Observed	Redd	8	96	104
D50	0.43						
D85	1.0					% Correct	84
SG	0.0						

Ferry Swale							
Canonical correlation		0.62	Predicted				
F-to-Remove			Non-Redd	Redd	Total		
Depth	22.1		Non-Redd	39	18	57	
Vel	29.9		Observed	Redd	5	47	52
D50	0.8						
D85	1.4					% Correct	79
SG	2.7						

Four Mile Bar							
Canonical correlation		0.46	Predicted				
F-to-Remove			Non-Redd	Redd	Total		
Depth	79.9		Non-Redd	146	74	220	
Vel	0.3		Observed	Redd	29	184	213
D50	1.0						
D85	6.4					% Correct	76
SG	0.3						

All Sites Combined							
Canonical correlation		0.45	Predicted				
F-to-Remove			Non-Redd	Redd	Total		
Depth	155.5		Non-Redd	215	157	372	
Vel	0.0		Observed	Redd	43	326	369
D50	0.0						
D85	6.4					% Correct	73
SG	0.3						

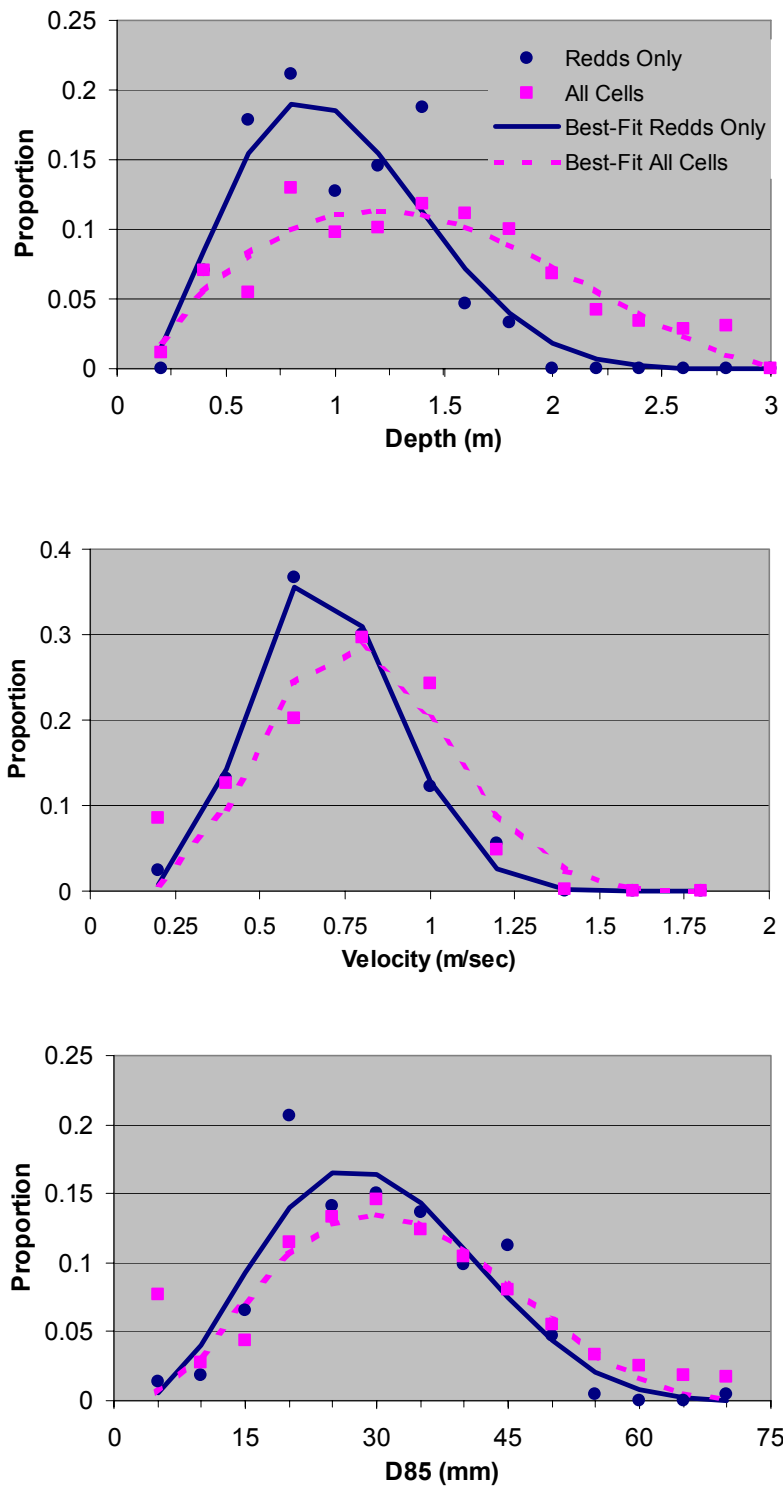


Figure 3.1. Proportion of all grid cells (magenta) across a range of depth, near-bottom velocity, and D85 categories at a) Four Mile Bar, b) Ferry Swale, and c) Powerline Bar and proportions for cells in these categories where a redd was present during the March survey (blue). Depth and velocity statistics are based on measurements taken at 20 kcfs at Four Mile and Powerline Bars, and at 5 kcfs at Ferry Swale, the assumed discharges when the March redds were excavated at these sites.

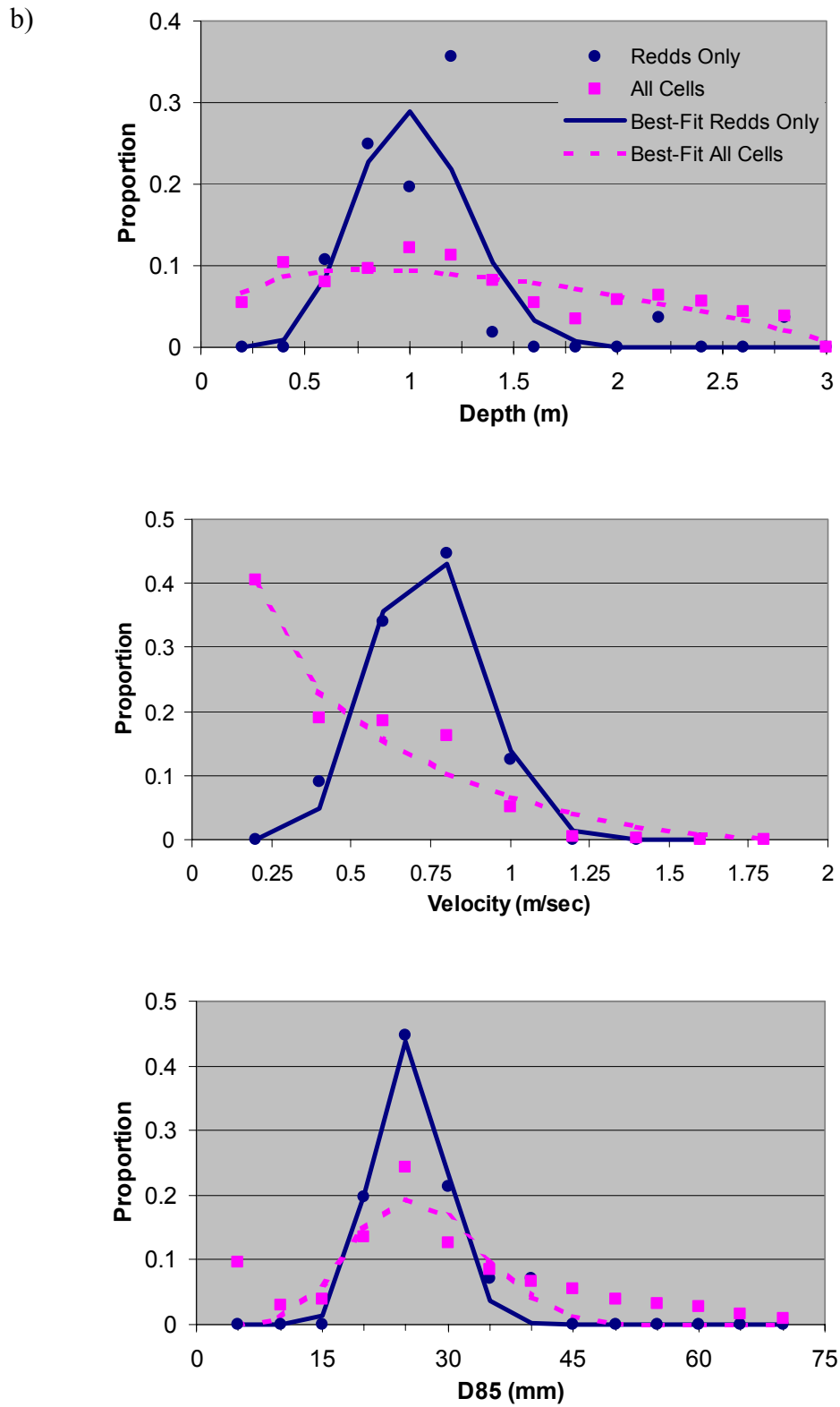


Figure 3.1. Con't (Ferry Swale).

c)

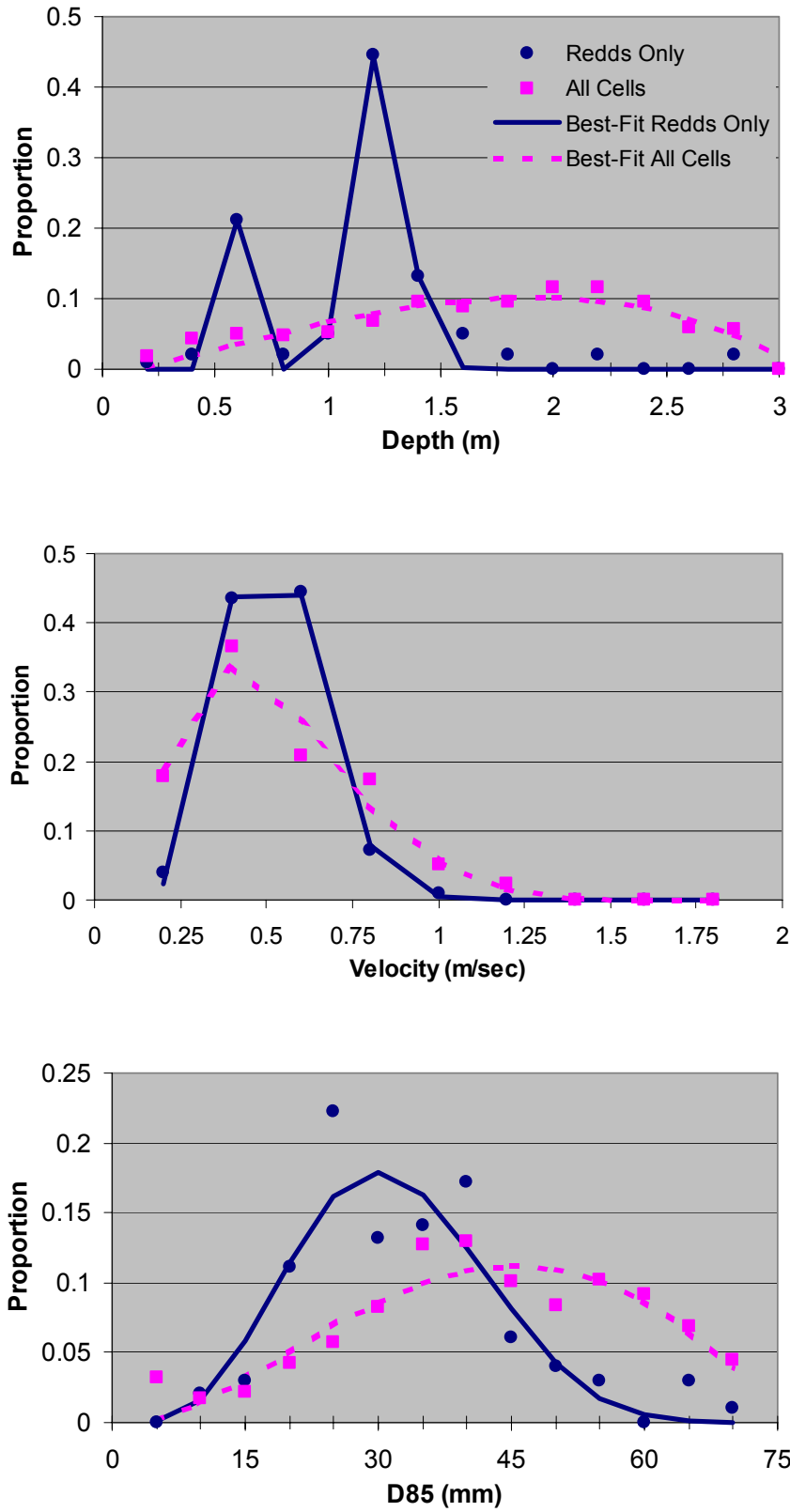


Figure 3.1. Con't (Powerline Bar).

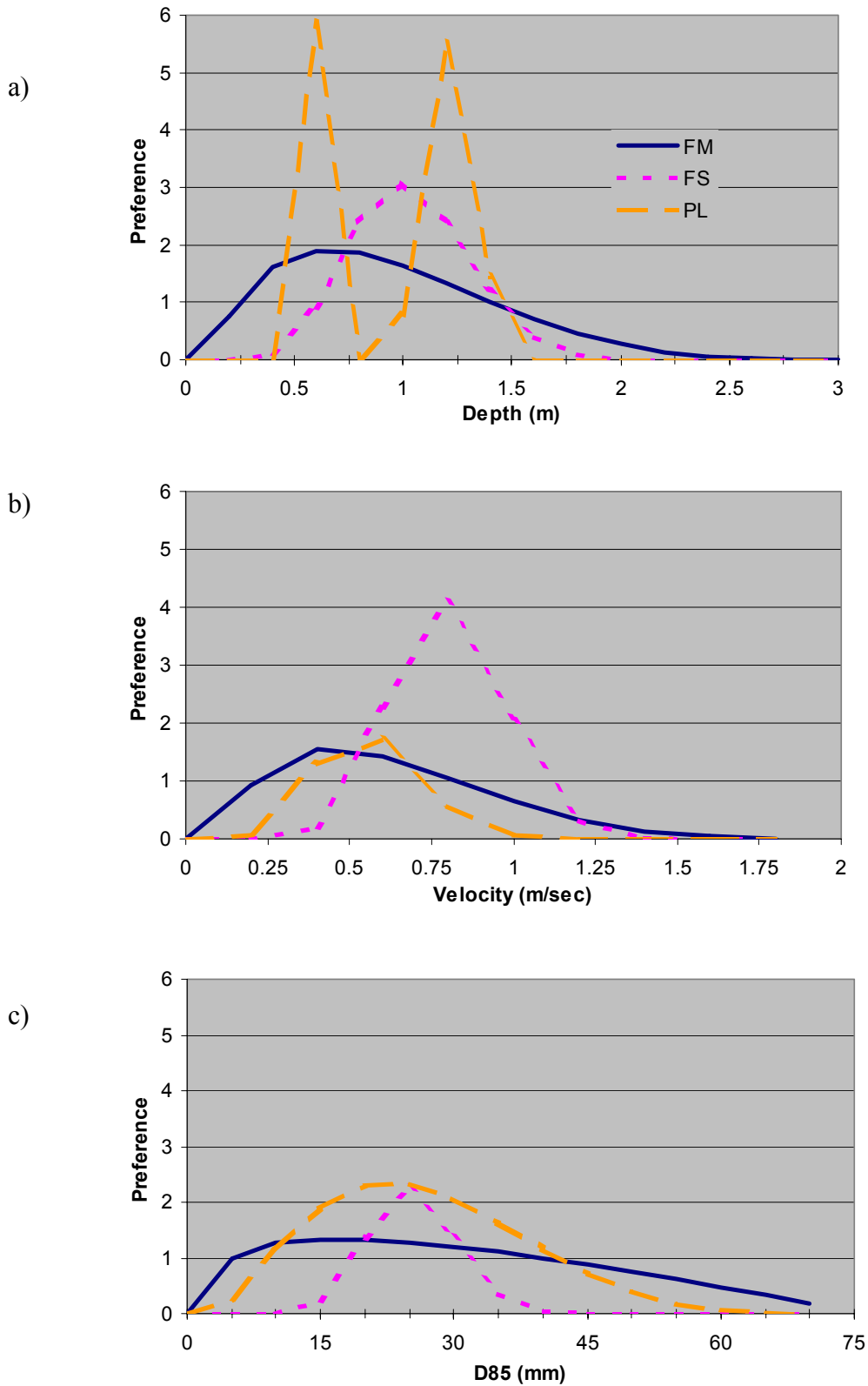


Figure 3.2. Comparisons of preference for a) depth, b) near-bottom velocity, and c) D85 at Four Mile Bar (FM), Ferry Swale (FS), and Powerline Bar (PL). Curves are the most likely Beta distribution models fit to the ratio of the number of cells with redds to the total number of cells in that depth, velocity, or D85 category.

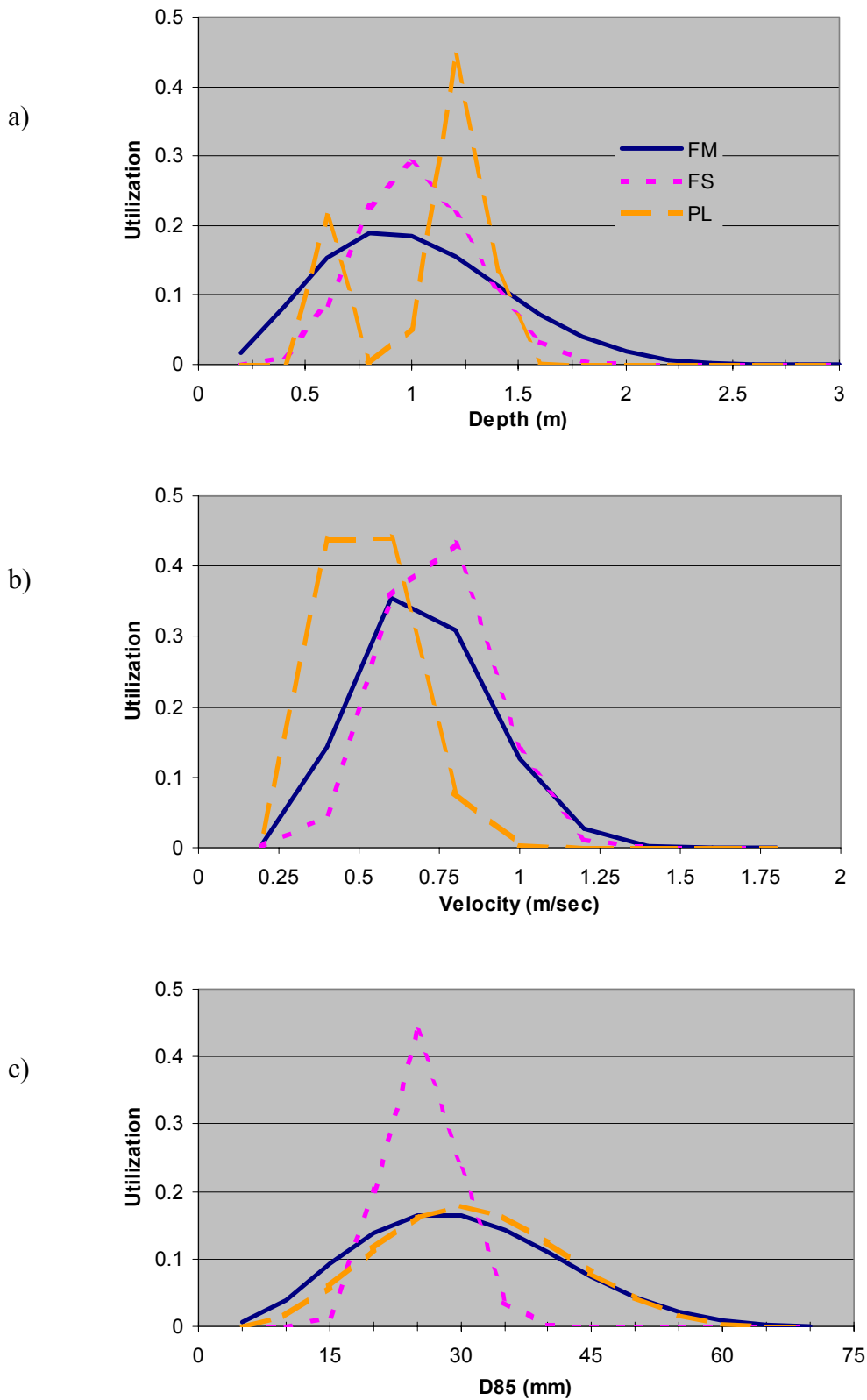


Figure 3.3. Comparisons of the spawning habitat utilization as a function of a) depth, b) near-bottom velocity, and c) D85 at Four Mile Bar (FM), Ferry Swale (FS), and Powerline Bar (PL). Curves are the most likely Beta distribution models fit to data from grid cells with redds at each site (blue lines in Fig. 3.1).

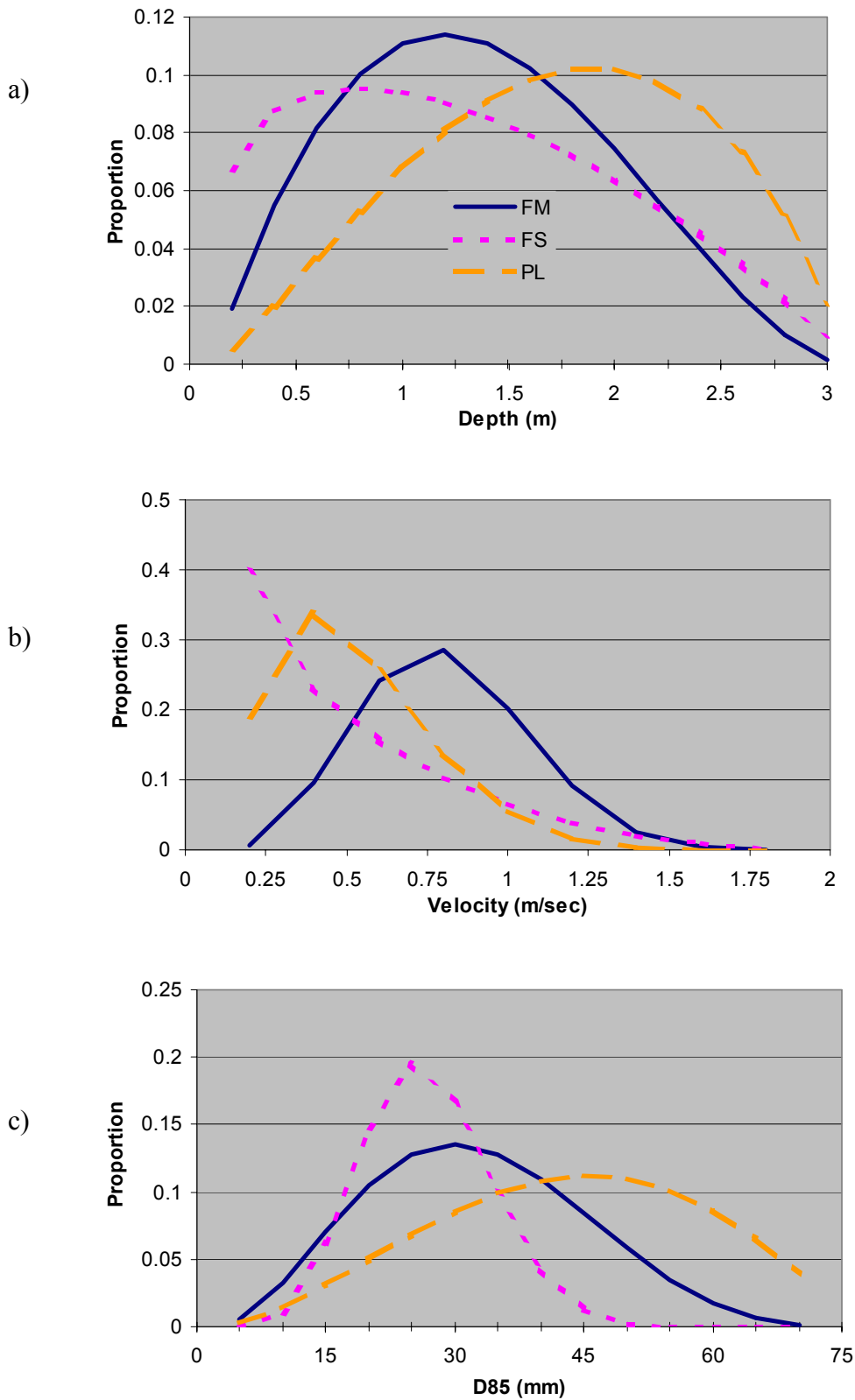


Figure 3.4. Comparisons of the availability of a) depth, b) near-bottom velocity, and c) D85 at Four Mile Bar (FM), Ferry Swale (FS), and Powerline Bar (PL). Curves are the most likely Beta distribution models fit to data from all grid cells at each site (magenta lines in Fig. 3.1).

exception that areas with very fine ($D_{85} < 5 \text{ mm}$) or large particles ($D_{85} > 45 \text{ mm}$) were avoided. Differences in preference among sites and among variables within-a-site generally reflected the patterns seen in the discriminant function analysis; Particle size tended to be a relatively unimportant variable at most sites; Depth was an important variable at Powerline and Four Mile Bars; Velocity was a very important variable at Ferry Swale and moderately important at Powerline Bar.

Habitat preference relationships were determined from the ratio of utilization to total habitat availability. The site boundaries of our study sites were delineated based on geomorphic features (gravel bars, pool tail-out, etc.). When comparing preference relationships among sites it is important to realize that site boundaries, which control the distribution of total habitat availability, will affect the preference relationships. It is therefore necessary to examine both utilization (Fig. 3.3) and availability (Fig. 3.4) relationships when commenting on differences in habitat preference among sites. For example, we saw a noticeable difference in preference for D_{85} between Four Mile and Powerline Bars (Fig. 3.2c) even though utilization was almost identical (Fig. 3.3c). Differences in the availability of D_{85} among these sites (Fig. 3.4c) were therefore the cause for differences in preference. It would be wrong to conclude that the preference curve for D_{85} at Four Mile Bar suggests that substrate is not an important component of spawning habitat. The correct inference is that D_{85} is an important determinant of spawning habitat, but that it is not 'preferred' at Four Mile Bar because there is a lot of sediment that has a grain size within the preferred range. The same reasoning explains differences in near-bottom velocity preference between Ferry Swale and Four Mile Bar. The lack of strong preference for near bottom velocity at Four Mile Bar is driven by the fact that the distribution of available velocities (Fig. 3.4b) nearly matches the utilization pattern. The availability of highly utilized velocity and substrate conditions at Four Mile Bar is probably a good part of the reason why it is the largest spawning site in Glen Canyon (Table 2.5).

Spatial patterns in predicted habitat preference at the redd-forming discharges for Four Mile Bar, Ferry Swale, and Powerline Bars were compared to redd locations (Fig.

3.5). The good correspondence between high preference and redd density is not an independent test of the models predictive ability since these same redd locations were used in the calculation of the preference models in the first place. However, one interesting characteristic of the maps are the areas that showed relative high preference coupled with low redd density. This pattern was statistically reflected in the discriminant function analysis through the number of false-positives (incorrect determination that a cell contained a redd when it did not). As previously mentioned, this could indicate either underutilization of spawning habitat or incomplete model specification. Highly preferred habitat with low redd densities tended to occur at the downstream ends of the gravel bars of all three sites. Many salmonid species have been observed to preferentially spawn where stream water down-wells into the gravel bed (Kondolf 2000). Down-welling will often be greater at the upstream side of gravel bars where the hydraulic gradient is largest. Upstream portions of the gravel bars may have been preferentially used relative to downstream areas with similar habitat conditions due to this factor. The spatial pattern in model error may in part reflect failure to include a variable which accounts for variation in down-welling across the bar surface.

Increased discharge resulted in higher total spawning habitat availability at Four Mile and Powerline Bars where suitable spawning habitat was located at higher stages (Fig. 3.6). Increased discharge reduced spawning habitat availability at Ferry Swale where the majority of habitat was located in deeper water. At Four Mile Bar, the total wetted area increased by a factor of 2 as discharge was increased from 5 – 20 kcfs (Table 3.2) while weighted useable area increased by almost five-fold. At Powerline Bar, total wetted area across this same discharge range increased by 1.4-fold while WUA increased over 9-fold. Increasing discharge at these high elevation gravel bars resulted in a disproportionate increase in spawning habitat availability. As discharge increased so did the proportion of spawning habitat at higher elevations (Fig. 3.5a and c). Predictions of WUA by stage at the redd-forming discharge of 20 kcfs closely matched the observed vertical distribution of redds during the March 2004 survey. While this is not an independent test of the model, it is comforting that the vertical distribution of WUA predicted by the models matches the pattern in redd hypsometry.

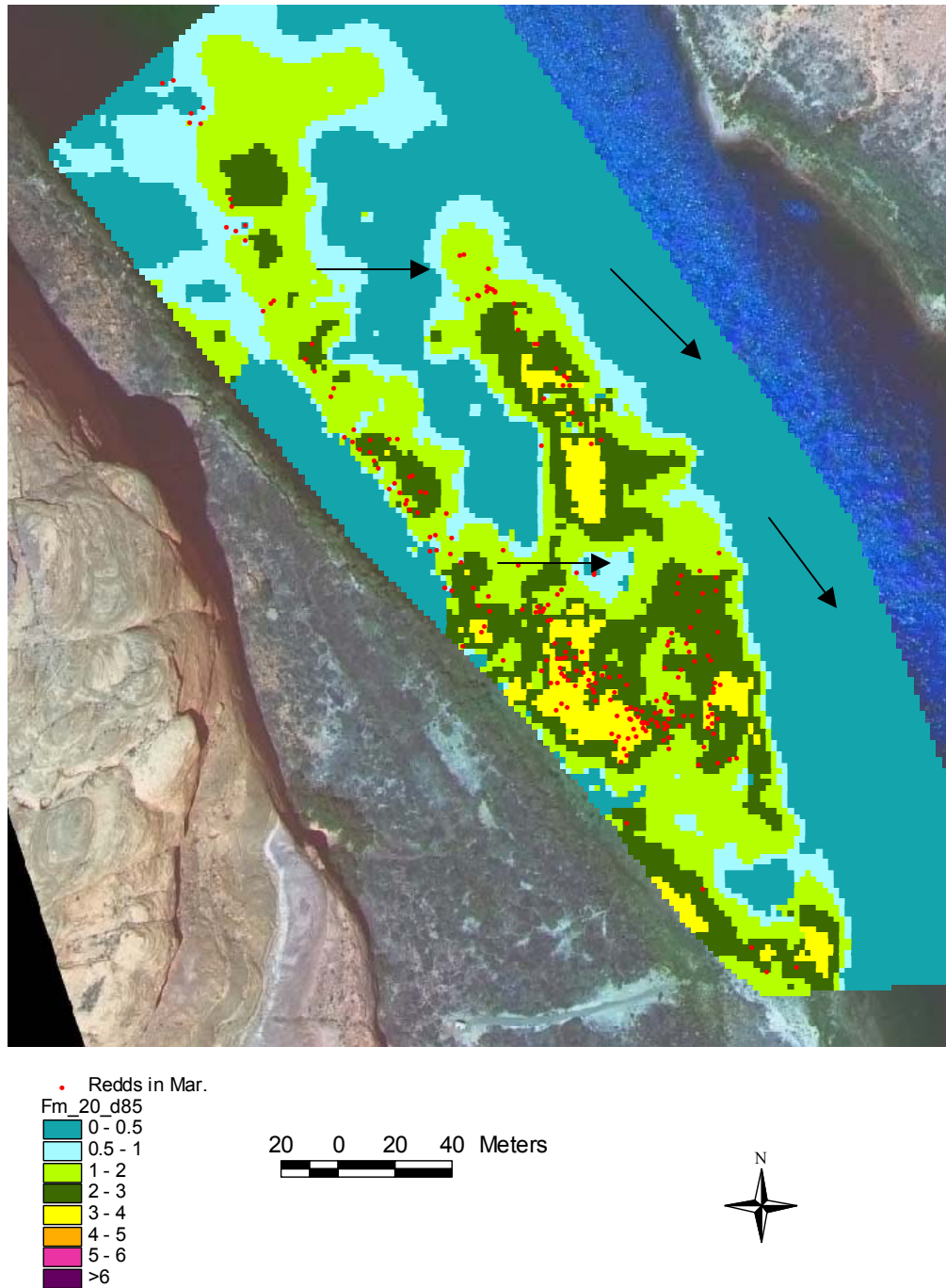


Figure 3.5. Maps of predicted habitat preference at a) Four Mile Bar at 20 kcfs (above), b) Ferry Swale at 5 kcfs, and c) Powerline Bar at 20 kcfs based on the product of preferences for depth, bottom velocity, and D85. Location of redds during the March survey, from which habitat preferences were developed, are also shown. Black arrows show the direction of water flow.

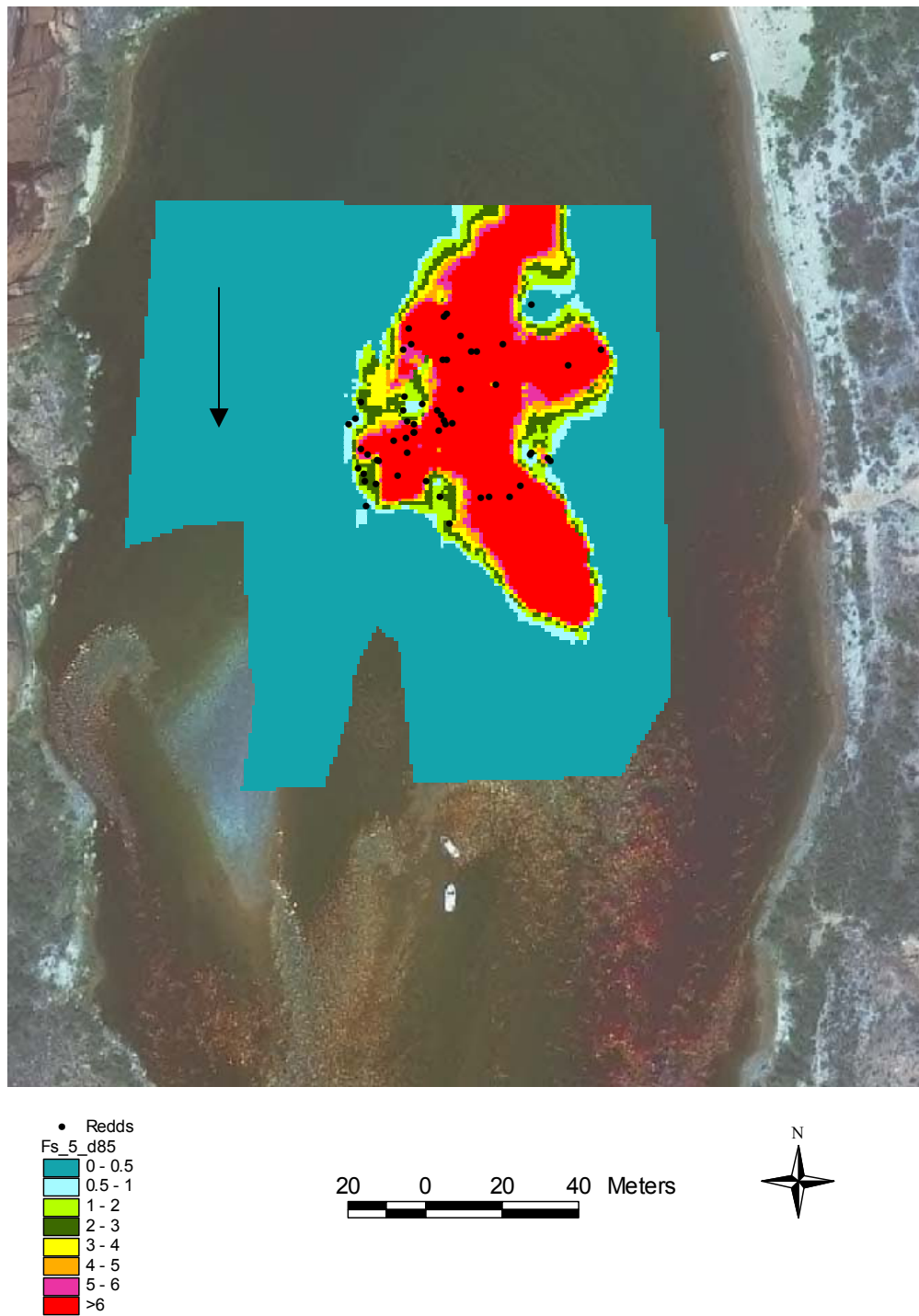
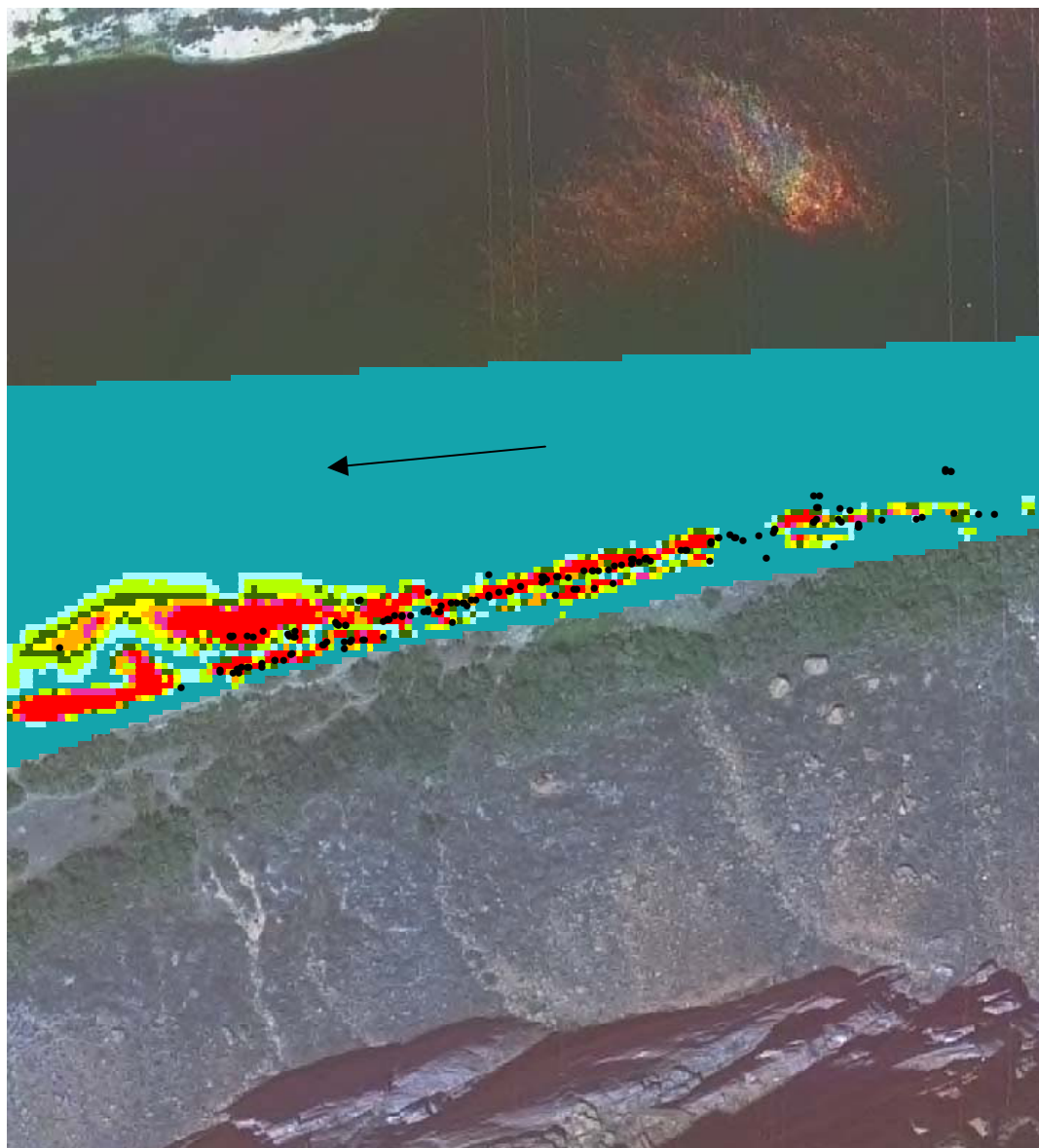


Figure 3.5. Con't (b) - Ferry Swale)



● Redds in Feb. and Mar.

PI_20_d85a



20 0 20 40 Meters



Figure 3.5. Con't (c) Powerline Bar).

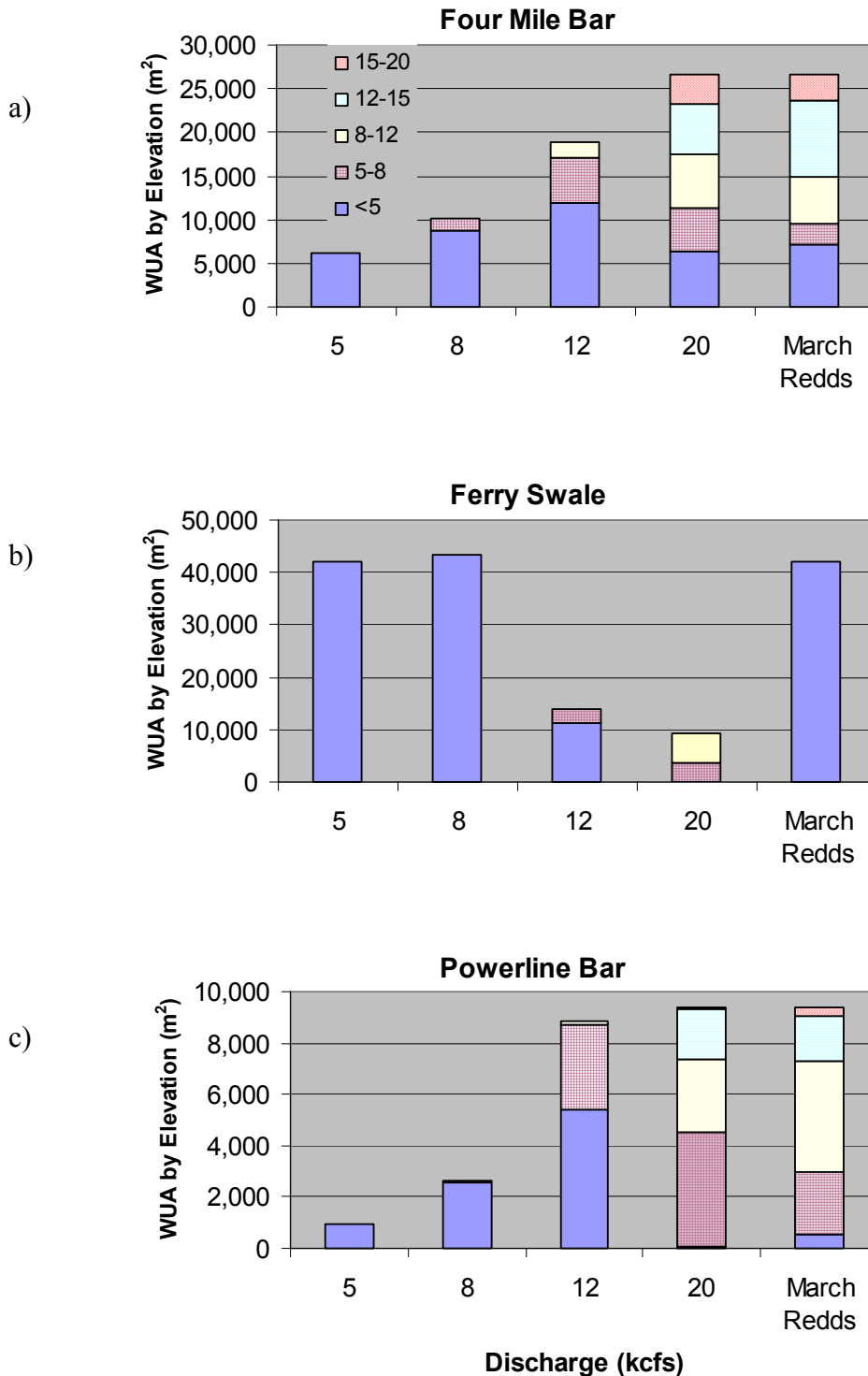


Figure 3.6. Predictions of Weighted Useable Area (WUA) at 5 stages (expressed in discharge units of kcfs) at four discharges (x-axis) at a) Four Mile Bar, b) Ferry Swale, and c) Powerline Bar. The total WUA across stages is equivalent to the bar height in the graphs. Also shown is the distribution of redds over the same stages from the March 2003 survey (from Fig. 2.6). The redd distributions should be compared to the distribution of WUA at 20 kcfs at Four Mile and Powerline Bars, and at 5 kcfs at Ferry Swale. These discharges are the assumed flows that the redds were created at.

3.3 Conclusions from Spawning Habitat Preference Study

The rainbow trout spawning habitat preference component of this study represents a significant effort relative to the magnitude of habitat use studies conducted in most other river systems. We estimated habitat preference at three large sites and characterized depth and velocity fields at four levels of discharge. In other studies, depth and velocity fields are usually estimated using a multi-dimensional model calibrated to a single level of discharge. The use of an underwater video camera to quantify particle size on the bed represents a significant improvement relative to other habitat studies where particle size is almost always roughly determined based on uncalibrated visual categorization.

Depths of 0.5 – 1.5 m, velocities of 0.3 – 1 m/sec, and D85 values of 15-45 mm are preferred by rainbow trout spawning in Glen Canyon. These statistics are reasonably close to the depth (0.3 – 0.8 m) and average velocity (0.3 – 1.0 m/sec) ranges reviewed in Montgomery and Tinning (1993). The D50 estimates of spawning areas in Glen Canyon reported by Kondolf et al. (1989) and Angradi et al. (1992) of 10 mm and 46 mm, respectively, bound the range of D85 values of sediments that were utilized for spawning in our study. It is important to note that the range of spawning depths we observed at the intensive monitoring sites where habitat measurements were taken underestimates the maximum depth where spawning was observed during the RAT surveys. In these surveys (Section 2), we found many sites (Table 2.5) where the depth of redds was 1-2 m and we observed spawning activity and redds in water greater than 3 m deep. Two inferences can be made from these observations: 1) the depth preference curves we developed from a limited number of sites are not representative of all spawning sites in Glen Canyon; and/or b) depth is not the physical variable that trout are using to select locations for spawning. It is possible that locations on gravel bars with shallow depth more often than not have the appropriate velocities or grain sizes and/or tend to be in areas where down welling is greatest.

The spawning habitat preference models developed for Glen Canyon were useful for evaluating the extent to which increased discharge during the January through March

experimental flow altered the elevations where spawning occurred. Weighted useable area computations showed that higher discharges increased total spawning habitat availability at sites that had available spawning habitat at higher stages such as Four Mile and Powerline Bars, and reduced spawning habitat availability at deep water redd sites such as Ferry Swale. The model also showed that the stage of spawning at Four Mile and Powerline Bars was increased under higher discharge. Such changes in spawning habitat availability would likely increase the proportion of redds that would be dessicated and the duration of exposure resulting from flow fluctuations. The redd hypsometry study showed that there was a high proportion of redds excavated in deep-water that would not be dewatered at flows as low as 5 kcfs. The large decline in spawning habitat availability at Ferry Swale under high discharge suggests that spawning at deep-water sites could be suppressed through maintenance of high flows although this prediction needs to be verified by direct field observations. As 40-50% of the redds in Glen Canyon are formed at stages below 5 kcfs, resolving this uncertainty is important if enhanced fluctuations, with the aim of increasing incubation mortality, are to be continued.

As with any habitat preference study, results from our spawning habitat work must be interpreted with caution. We developed preference curves for each site based on a single discharge. When we predicted WUA as a function of discharge, we assumed that the preference relationships were stationary with respect to discharge. Other studies have shown that habitat availability-discharge relationships do not always meet this assumption (e.g., Pert and Erman 1994). In many WUA studies there is often an implicit assumption that changes in habitat availability have some type of population-level effect. Even if one believes that habitat preference is stationary with respect to discharge, we have no data to evaluate whether reductions in spawning habitat availability reduce the total egg deposition in Glen Canyon or the survival of eggs and alevins. We have avoided this issue by only using WUA calculations to estimate how discharge potentially influences the stage where spawning occurs. This has relevance for designing flow regimes that are more effective at increasing the percentage of redds which are exposed due to fluctuating flows. We make no claims regarding the linkage between WUA predictions and impacts on recruitment of young trout. These impacts must be assessed

through direct measurements of rainbow trout juvenile and adult life stages in Glen Canyon.

4.0 Seasonal and Spatial Trends in Length Frequencies and Growth Rates of Young-of-Year Rainbow Trout in Glen Canyon

It is generally believed that the year-class strength of fish populations is determined by growth and survival of fish in their first year of life. Improving our understanding of recruitment, growth and survival of Young-of-Year (YoY) rainbow trout below Glen Canyon Dam should therefore help define and evaluate specific management strategies targeted at regulating incubation and post-emergent survival rates. The increased daily fluctuations in discharge of the January to March 2003 and 2004 experimental hydrographs were designed mostly to increase the mortality of young-of-year (YoY) rainbow trout. YoY stream-dwelling salmonids prefer near-shore habitats that are shallow with low-velocities and abundant cover (Montgomery and Tinning 1993). Daily variation in discharge will result in lateral shoreline movement that can cause stranding of juvenile fish, or lead to sub-lethal impacts related to increased stress levels, predation risk, energy expenditure, or reduced feeding opportunities (Cushman 1985). Published data on the impacts of sub-lethal effects of fluctuating flows are limited and must be inferred from studies on habitat use and physiological stress. Vehenan et al. (2000) observed that juvenile brown trout used higher nose velocities with increasing water flow and did not fully compensate for increased energy expenditures by changing microposition. Shirvell (1994) reported that fish initially responded to increased flow by moving closer to the streambed and then, if necessary, by moving laterally to seek out appropriate velocity conditions. Flodmark (2002) showed that daily variation in discharge did not seem to affect adult fish stress levels when peaking was a regular occurrence.

In contrast to the lack of data on sub-lethal effects of daily variation in discharge on juvenile fish, there are many observations of direct impacts caused by stranding. Factors that control the extent of stranding at a given site include riverbank profile, substrate type, fish size and age, species, time of day, exposure frequency, season, temperature, and the rate of stage change. The extent of stranding appears to be highest in low-angle habitats with abundant cover (Halleraker et al. 2003). Small brown trout YoY (ca. 50 mm) have been shown to be more vulnerable to stranding than larger juveniles

(75-90 mm). Stranding rates tend to increase at lower water temperatures and are highest if flow reductions occur during daylight hours (Bradford et al. 1995, Saltveit et al. 2001). A decrease in the down-ramping rate from 60 cm/hr. to 10 cm/hr was shown to reduce stranding of brown trout YoY by 50% (Halleraker et al. 2003). The down-ramp rate in Glen Canyon during the January to March experimental flow period was approximately 15 cm/hr. Stranding rates have been shown to increase following a long habituation to steady flows (Halleraker et al. 2003). Stranding of small juveniles (ca. 50 mm) may be difficult to observe in the field. A 1-hr. search of a 75 m² area by two technicians found less than 40% of the total fish known to be stranded in an enclosed area (Saltveit et al. 2001).

In this study, we measured changes in length-frequency and relative abundance of YoY rainbow trout in Glen Canyon from April through December in 2004 and from June through October in 2003. These data provided information on spatial and temporal trends in YoY abundance. A comparison of length-frequencies over time and among habitat types was used to make inferences regarding the seasonal timing of recruitment of newly emerged fish to the YoY population, survival, growth, and movement among habitat types. We analyzed the microstructure of otoliths from a subsample of fish to establish a length-age relationship and to evaluate the effects of dam operations on YoY growth. The combined catch and age information were used to back-calculate a hatch date distribution that was compared with the distribution estimated from redd counts and the egg mortality model (Section 2.0) to determine whether there were differences in survival rate over the incubation period.

4.1 Sampling and Analytical Methods for Young-of-Year Study

The YoY study consisted of two components. Field survey methods are described in Section 4.1.1. Analysis of otolith microstructure was used to estimate YoY age, make inferences on effects of fluctuating flows on growth, and, in conjunction with fry survey

data, to back-calculate the hatch date distribution. Methodologies for this analysis are described in Section 4.1.2.

4.1.1 Methods for Young-of-Year Field Surveys

Rainbow trout YoY were sampled by backpack and boat electrofishing on a near-monthly basis in Glen Canyon from April to December in 2004 ($n = 8$ trips) and from June to October in 2003 ($n = 4$ trips). We classified shoreline units from the GCMRC shoreline habitat coverage (Mietz 2003) into low angle (cobble bars, sand bars, debris fans) and steep angle (talus) habitats. Twenty random units were selected from each group and sampled by backpack and boat electrofishing, respectively (Table 4.1). The sampling followed a repeated measures approach in that the same 40 units were sampled each month. Note that in 2003, only 20 low angle sites were sampled by backpack electrofishing. A limited amount of boat electrofishing was conducted in steep habitats in 2003 to establish sampling methodologies. The GCMRC shoreline coverage divides the 56 km of shoreline in Glen Canyon into a total of 95 habitat units that range from 275-600 m in length. We sampled 30-50 meters of shoreline within each of the 40 randomly selected units.

Upon arrival at a low angle site, a 30-meter length was measured with a survey tape or laser range finder, and upstream and downstream limits marked with fluorescent glow sticks. Starting at the downstream end of the site, two fisheries technicians systematically worked their way upstream catching all fish within 2.5 meters from the shoreline using a backpack electrofisher (Smith-Root Model 12B). Electrofisher settings were set at 200 volts, a frequency of 90 Hz, and a pulse width of 8 milli-seconds. One technician operated the backpack electrofisher and the other captured fish with a small dipnet and illuminated the area near the anode with a battery-powered Q-beam spotlight (ca. 1 million candlepower). At steep angle sites, a 50-m length was measured with a survey tape or a laser-range finder and the boundaries marked with fluorescent glow sticks. An Osprey 4.6-m aluminum boat with a 50 Hp motor outfitted with a Smith-Root electrofishing unit and 5,000 watt generator was used to sample a shoreline width of 2.5 m.

Table 4.1. Locations of Young-of-Year electrofishing sites in Glen Canyon in low and steep angle habitats. Site locations are from the GCMRC shoreline habitat coverage with the identifier denoting shoreline type (sand bar=SB; cobble bar=CB; debris fan=DB; talus=TA), distance in miles from Lees Ferry, and right (R) or left (L) bank. “*” denotes sites with additional sampling in July 2004 at the daily maximum and minimum discharge during night and day. All other sites were only sampled during the daily minimum discharge at night. Steep angle shorelines in 2003 were only sampled during September and October trips.

Site No.	2003		2004	
	Low	Steep	Low	Steep
1	CB-15.2R		SB-15.0R*	TA-14.7R*
2	CB-14.3R	TA-14.3L	CB-14.3R	TA-14.3L
3	CB-13.8L		CB-13.8L*	TA-13.6R*
4	CB-13.0R		SB-13.6L*	TA-12.9L*
5	CB-12.2L		SB-13.2L*	TA-12.1R*
6	CB-11.8R		CB-12.2L	TA-11.7R
7	CB-10.8R	TA-10.8L	CB-10.8R*	TA-10.8L*
8	CB-10.0R		SB-8.5R*	TA-10.3R
9	CB-8.1L	TA-8.8L	SB-7.6L	TA-7.8L*
10	SB-7.1L	TA-7.8L	SB-6.3R	TA-7.2R
11	SB-5.6L		CB-5.3R	TA-6.5R
12	CB-5.3R	TA-5.1L	CB-4.1RU/S	TA-6.0R*
13	CB-4.1RU/S		CB-4.1RD/S*	TA-5.5R*
14	CB-4.1RD/S		SB-3.4R*	TA-5.0R
15	SB-4.0L		DB-2.3L*	TA-4.8L*
16	SB-3.4R		SB-2.3R*	TA-4.3R
17	DB-2.3L	TA-2.8L	DB-2.1L*	TA-2.8L*
18	DB-2.1L		SB-0.9L	TA-2.5R*
19	TA-1.4R		SB-0.6L*	TA-1.4R*
20	SB-0.6L		SB0.0R	TA0.0L

The boat electrofishing crew consisted of one driver and one dipper at the front of the boat. The Smith-Root boat electrofisher was set at ‘CPS-High’ and the power was adjusted at each site to produce a current of approximately 16-18 amperes and 200 volts. Every effort was taken to ensure that thoroughness and technique were consistent among sites and sample periods. On average, 500 seconds of electrofishing effort was required to fish a 30 and 50 m length of shoreline habitat based on backpack and boat electrofishing,

respectively. All sampling was conducted at night at a flow that was within 1 kcfs of the daily minimum discharge. Typically, ten sites were sampled per night between 23:00 - 6:00.

Upon completion of electrofishing, fish were anesthetized using clove oil and the forklengths of all fish were measured to the nearest mm. Following recovery, the majority of fish were released back into the site. A length-stratified subsample of fish were sacrificed and preserved in 95% ethanol. Ten depth and velocity measurements, systematically distributed along the length of the site at 1.5-m from the wetted edge, were taken using a Swoffer Instruments current meter and topset wading rod. Velocities were measured at 60% of the total depth to estimate the average water column velocity. Depth and velocities were not measured during the November and December sampling sessions as the minimum flows during these trips were very similar to those in other sessions (Fig. 1.2). Shoreline gradient was measured during the July sample period using a survey tape, stadia rod, and Abney level.

The effects of discharge and time-of-day on catch rates of YoY were investigated. Twelve of the 20 randomly selected habitat units for both low and steep angle habitats (Table 4.1) were divided into four 30 and 50 m sections, respectively. Each section was sampled at one of the following four discharge-times of day combinations: daily maximum discharge – daytime; daily maximum discharge- nighttime; daily minimum discharge – daytime; and daily minimum discharge - nighttime. Sampling was conducted between June 30 and July 5, 2004. Differences in catch rates caused by time of day and discharge were evaluated using a paired t-test where sections within a site were considered repeated measures. The analysis was performed independently for both backpack and boat electrofishing gear types.

4.1.2 Methods for Analysis of Otolith Microstructure for Ageing Young-of-Year

A subsample of YoY fish captured on each trip were preserved in 95% ethanol and sent to a laboratory (www.mar.dfo-mpo.gc.ca/science/mfd/otolith/) for examination of otolith microstructure. The otoliths of teleost fish contain growth increments that are deposited with a daily periodicity (hence the term "daily ring"), thus providing precise age and growth information through much of the first year of life (Campana and Nielson 1985). Fish selected for ageing were randomly subsampled from the total catch on each survey using a length- and habitat-stratified design: within each sample period, 5 fish were randomly taken from low angle sites, and 5 from steep sites, for each 10-mm length category. Beginning in August 2004, sample size was reduced from 5 to 3 fish per length-habitat category due to budget constraints. In 2003, when only low angle habitats were selected, 10 fish per length category were sampled.

The forklengths of preserved fish were measured in the laboratory prior to dissection. Both sagittal otoliths were removed from each fish and mounted individually on microscope slides in cyanoacrylate glue. Otoliths were polished close to the mid-plane, flipped and re-glued, then polished to the growth plane with 30 μm and 3 μm lapping film, as per established procedures (Stevenson and Campana 1992). All otoliths were examined at a magnification of 400-1250x under a compound microscope. Using the well-defined hatch check as a reference point, daily increments between the hatch check and edge were counted 2-4 times in at least one otolith of each pair (Campana 1992). The resulting count was recorded as the age from hatch to capture.

The validity of daily increment counts as accurate age indicators in young fish is well established (Campana and Neilson 1985). However, to insure accuracy in this application, we compared estimates of age derived from otoliths for a small sample of hatchery YoY where age was precisely known. As part of a normal hatchery operation, wild spawning rainbow trout were removed from their natal stream (Blackwater River, BC) and spawned in a B.C. hatchery on May 13, 2003. Eggs were reared under constant temperature (7 C) and moved to a feeding trough (10 C) at swim-up. Fish were sampled

from the trough at 31 and 84 days after hatching and preserved in 95% ethanol. Otoliths from these fish were removed and the known number of days from hatch to sampling was compared to the estimates derived from the daily ring counts between the hatch check and the otolith edge. This was a blind-analysis as the age of fish was unknown to the technicians at the time they examined the otoliths.

In older fish captured in Glen Canyon, there was often a very pronounced broad white check 20-60 days outside of the hatch check. The check was characterized by a very light band comprising several poorly-contrasted daily increments, and occasionally by reduced increment widths. In a subsample of fish, increment counts between hatch and the white check, and between the white check and the edge, were recorded. The distance between the hatch and the broad white check, and between the check and the edge, were measured along the longitudinal axis of the otolith. Measurements ($\pm 1 \mu\text{m}$) were made with an image analysis system working at a resolution of 1280 x 1024.

In 2003, a random subsample of 90 fish were measured in the field, preserved individually in 95% ethanol for 1 month, the ca. time between preservation and otolith extraction, and then re-measured in the laboratory. The correlation between preserved and live forklengths was extremely high ($r^2 = 0.997$) and shrinkage of preserved fish averaged 1%. Prior to estimating the parameters of length-at-age models, laboratory forklengths were converted to field values based on this field-laboratory forklength relationship.

Logistic growth models were fit to the converted length - age data. The form of the model was,

$$(4.1) \quad L_t = \frac{L_\infty}{1 + e^{-K(t-t_0)}},$$

where L_t is the predicted forklength (of fish measured in the field) at age t (days from hatch), K is the instantaneous growth rate at the origin of the curve, L_∞ is the asymptotic

length, and t_0 is the age at the first inflection point of the curve which corresponds to the age of the maximum absolute growth rate (Campana and Jones 1992). Note that the absolute growth rate (g) of the logistic curve at age t is,

$$(4.2) \quad g_t = K * L_t * \frac{(L_\infty - L_t)}{L_\infty},$$

Most likely parameter estimates for the logistic model were calculated by minimizing the sum of squares between predicted and observed forklengths using a nonlinear iterative search procedure. The seasonal trend in egg hatch was estimated by predicting the age of all fish that were captured based on their forklengths by rearranging eqn. 4.1 to solve for t . The predicted age was then subtracted from the date of capture to calculate the date of hatch.

A striped pattern in increments was observed on the otoliths of many individuals in 2003. This visual pattern was identified by the presence of atypical daily increments (different appearance, usually light in color) formed every 7 days. For all otoliths, the presence or absence of the striping pattern was recorded. The number of otoliths where the presence of a striping was ambiguous was also recorded. To determine if the 7-day striping pattern was associated with periodic growth, a random sample of otoliths ($n = 15$) from 2003 with a clear striping patterns were examined and digitally photographed at a microscopic magnification of 600x under oil immersion. Given the 1280 x 1024 resolution of the image analysis system, measurement accuracy was $\sim 0.1 \mu\text{m}$. The width of individual daily increments was measured as the distance between the midpoints of adjacent D zones (terminology of Kalish et al. 1995). Measurements were made perpendicular to the local growth axis, beginning at the D zone just medial to the white stripe, and proceeding distally. Increment sequences were measured only if every increment of the 7-day striping cycle was clearly defined.

4.2 Results from Glen Canyon Young-of-Year Study

4.2.1 Young-of Year Field Survey

Sample sites classified as low angle habitats had an average gradient of 11.6% compared to steep angle sites that had a gradient of 36.6% (Table 4.2). Low angle sites had depths and velocities that were typically 40% and 75% of those in steep angle habitats, respectively. In Glen Canyon, cobble bars, debris fans, and sand bars comprise about 50% of the total shoreline length while talus slopes make up 40%. Cliff habitats, which were not sampled, make up the remaining 10% of the shoreline length.

Spatial and seasonal differences in YoY density at low angle sites were reasonably consistent in 2003 and 2004 (Fig. 4.1). Densities were highest at low angle sites in the first 5 miles below the dam or the first 4 miles upstream of Lees Ferry. An obvious depression in densities was seen in the middle part of the reach, which has been observed for adult rainbow trout as well (McKinney et al. 1999). Peak densities in 2004 were higher than those in 2003. A very large decrease in density in low angle habitats between the late-July/early-August and September sampling periods was observed in both years. In talus shorelines sampled by boat electrofishing (steep angle habitats) an upstream-downstream gradient in density was observed. There was also less site-to-site variability than seen across low angle sites and a depression in densities in the middle section of the reach was not observed. Densities during the June sampling period were low as few YoY had recruited to steep habitats by this time. There was a substantial drop in densities between the November and December sample periods in steeper habitats. The December session occurred about 1 week after the 42.5 kcfs beach habitat building high flow event that ran from November 20-25, 2004.

There was a very strong effect of diurnal variation in discharge on catch rates. In low angle habitats, catch rates during the day at the minimum flow were 4-fold higher than during the daily maximum flow. At night, catch rates were 5-fold higher at the daily minimum discharge than at the daily maximum (Fig. 4.2). Based on a paired comparison

across sites, there was less than a 5% chance that these differences could be due to chance alone. At steep angle sites, catch rates at night during minimum flows were over 2-fold higher than at daily maximum flows, and over 3-fold higher at daily minimum flows during the daytime. These differences were significant at a Type I error rate of 1%.

Table 4.2. Physical characteristics of fry sampling sites in 2004 and discharge statistics. Statistics are the average monthly values of the daily minimum, average, and maximum flows. Also shown is the amount of shoreline length in the GCMRC shoreline GIS coverage by habitat type (CB=cobble bar, DB=debris fan, SA=sand bar, TA=talus, CL=cliff), and the percentage of shoreline length by the habitat type used in this analysis (low vs. steep).

		April	May	June	July	August	September
Discharge (kcfs)							
	Minimum	7.7	6.7	8.9	10.4	10.0	5.0
	Average	10.9	9.7	13.5	14.6	14.6	8.1
	Maximum	13.4	12.1	16.6	18.0	17.7	10.1
Depth (cm)	Hab. Type						
	Low	26	20	18	31	31	18
	Steep	53	71	55	65	61	64
Velocity (cm/sec)	Low	8.7	3.7	2.8	4.5	4.9	0.8
	Steep	6.4	4.5	5.9	7.5	7.5	2.0
Gradient (%)	Low				11.6		
	Steep				36.6		
Available Shoreline Habitat (km)							
	CB	DB	SA	TA	CL	Total	
Glen Canyon	10.2	1.1	16.5	21.5	6.9	56.3	
Marble Canyon	8.2	20.5	76.9	65.8	52.5	223.9	
% of Shoreline Habitat		Low	Steep				
Glen Canyon	49.4	38.2					
Marble Canyon	47.2	29.4					

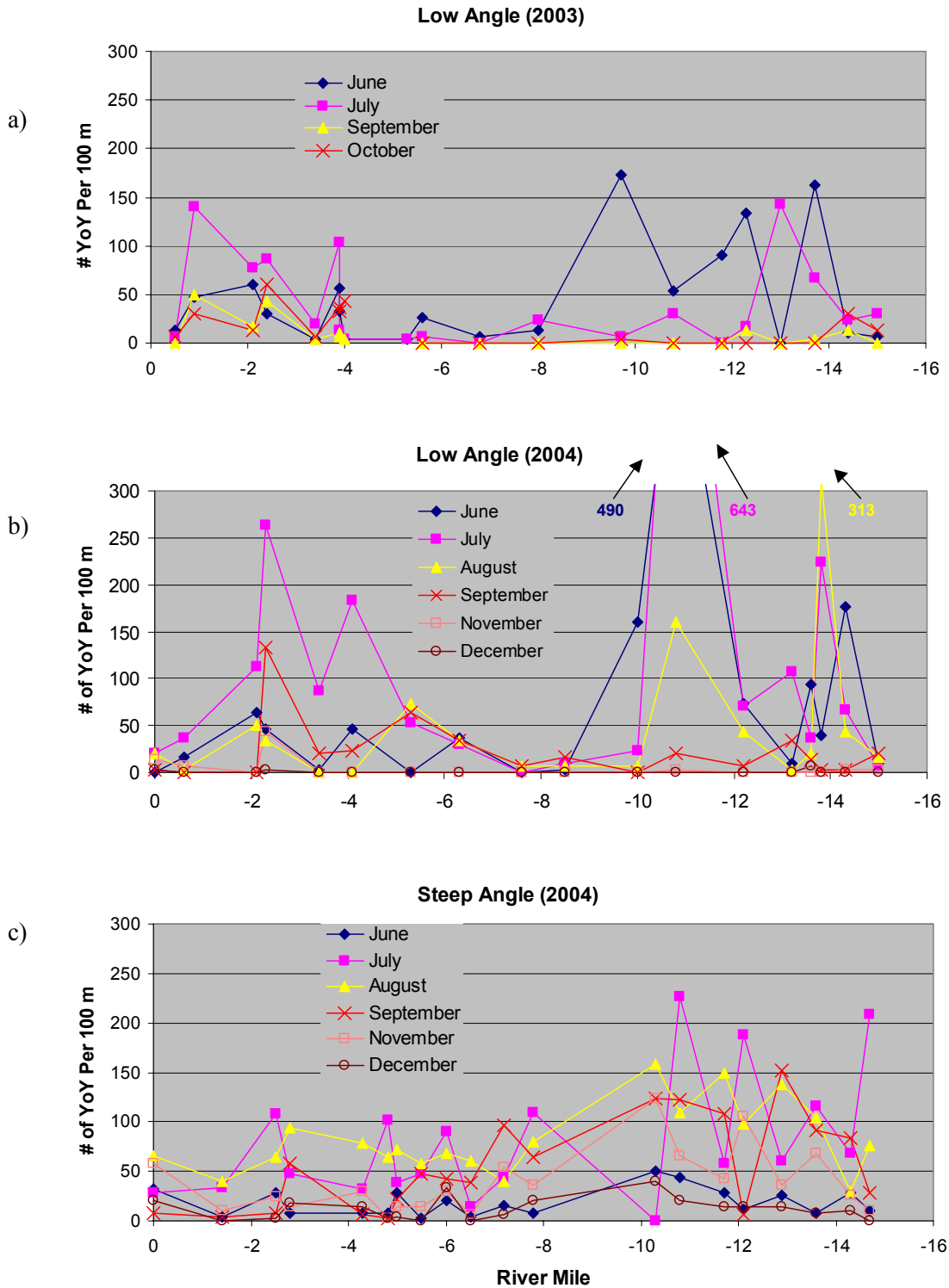


Figure 4.1. Spatial and temporal trends in YoY rainbow trout density in a) 2003 and 2004 in b) low and c) steep angle habitats. For clarity of presentation, densities during April and May in 2004 are not shown as there was no sampling conducted during these months in 2003. Densities in 2004 during these months were very low. Densities in low angle habitats in June, July, and August 2004, are off the scale and were 490, 643, and 313 YoY per 100 m, respectively. Glen Canyon Dam is located at river mile -15.6 and Lees Ferry is at river mile 0.

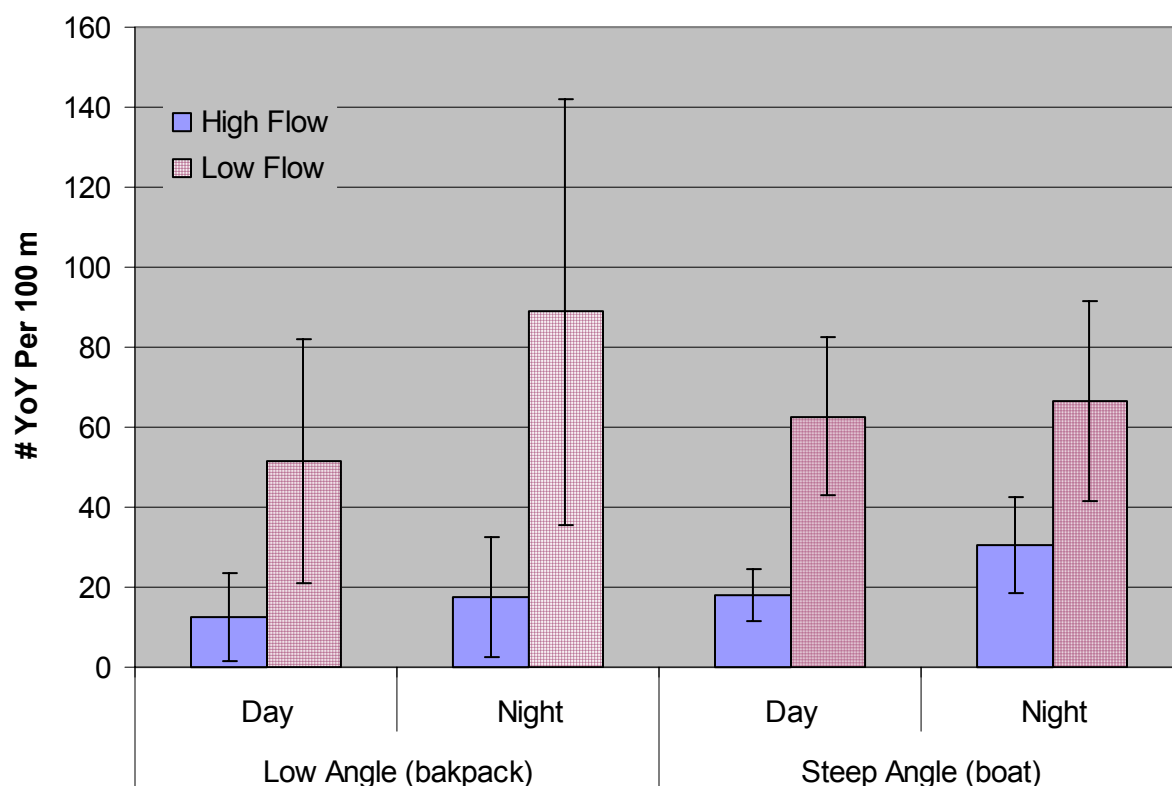


Figure 4.2. Density of YoY rainbow trout in Glen Canyon in steep and low angle habitats sampled during the daily maximum (High Flow) and daily minimum (Low Flow) flows during daytime and nighttime. Error bars denote 90% confidence limits.

Differences in catch rates between samples taken at maximum vs. minimum daily discharges could be due to differences in catchability rather than changes in the density of fish near the shoreline. The effect of light intensity on catchability was accounted for in the analysis by conducting sampling at night and during the day. In both habitats, catch rates at night were slightly higher than during the day, and this difference was greatest at low angle sites during low flow. However, night-day differences were not significant (Type I error = 0.05) for any of the cases. There were relatively minor changes in depth and velocity at maximum and minimum daily flows in the sampled habitat (Table 4.3). Average depth was 10-15 cm greater at the maximum daily discharge but the difference was only statistically significant in steep angle habitats. Average velocity was marginally

higher at the minimum daily flow in low angle habitats and marginally lower in steep angle habitats but neither difference was significantly different.

Table 4.3. Average depth (cm) and average water column velocity (cm/sec) for 12 low and steep angle sites sampled at maximum (Max. Q) and minimum (Min. Q) daily discharges in July 2004. The “Prob.” column is the probability that the mean difference in densities at maximum and minimum discharges is due to chance alone based on a paired t-test.

	Depth			Velocity		
	Max. Q	Min. Q	Prob.	Max. Q	Min. Q	Prob.
Low	39	29	0.06	3	7	0.10
Steep	75.5	60.6	0.03	12.1	5.6	0.11

The difference in catch rates between maximum and minimum daily flows estimated during July 2004 confirms anecdotal observations from May of 2003. When backpack electrofishing during the day in low angle habitats over the Memorial Day long weekend, when flows were held constant at 8 kcfs, we caught a large number of YoY fish and decided to begin our systematic fry survey on the following Tuesday when flows resumed to the normal weekday Modified Low Fluctuating Flow regime (7.4 – 12.4 kcfs). Despite considerable effort, we were unable to capture any fish during our day and night samples at high flows. From this observation we suspected that YoY were holding close to the daily minimum elevation and were not following the waters edge as discharged increased. All future sampling was therefore conducted at night at discharges near the minimum daily levels.

Comparison of length frequencies of YoY rainbow trout in Glen Canyon in 2004 across sampling sessions and habitat types shows effects of recruitment, somatic growth, mortality, movement, and vulnerability (Fig. 4.3). In low angle habitats small YoY, predominantly in the 30-35 mm length class, became vulnerable to capture in early-May. The analysis of otoliths microstructure (section 4.2.2) showed that it took at least 1.5 months from hatch before YoY became vulnerable to capture by electrofishing. The time

from spawning to hatch was ca. 33 days based on observed intergravel water temperatures of 10 C and a requirement of 329 accumulated thermal units (Section 2). Thus, the small fish we observed in early-May 2004 were produced from eggs deposited 2.5 to 3 months earlier, or around early-February. As there was very little spawning prior to this date (Fig. 2.4) it is not surprising that we did not capture any YoY in April from the 2004 cohort and relatively few fish in May.

The abundance of fish in the smallest, that is, youngest age category, was less than those of larger-older fish, even early in the season when the abundance of young fish must have been higher owing to the timing of hatch. This pattern indicates reduced vulnerability of very small fish to the sampling gear relative to larger fish. The peak abundance of small YoY fish in low angle habitats occurred during the June and July sampling sessions, corresponding to peak spawning in March and April. By August, YoY numbers were declining as mortality and/or movement exceeded the number of new YoY recruits entering the vulnerable population, and growth was also very apparent. The September length frequency shows the continued effect of growth and mortality/movement. There were very few fish present in low angle habitats during the November session and almost no fish were captured in December.

The length frequency trends in 2004 in the steep angle habitats were markedly different and suggest that colonization of steeper habitats is dependent on the density and growth of fish in lower angle habitats (Fig. 4.3). In May 2004 we observed low numbers of fish that were mostly greater than 110 mm. These fish would have originated from spawning from the late-spring or early-summer of 2003 (see Section 4.2.2). YoY from the 2004 cohort did not appear in steep habitats in substantive numbers until June. Density increased considerably between June and July and between July and August along with an increase in size. While steep habitats were utilized by YoY as small as 25-40 mm, YoY did not show up in substantive numbers until June even though they were present in Glen Canyon at least a month before, as evidenced by the May length frequency from low angle habitats. The large increase of YoY in steep habitats between

June and July occurred only after high densities were reached in low angle habitats. This suggests that the rate of movement of very young fish from low to steep angle habitats

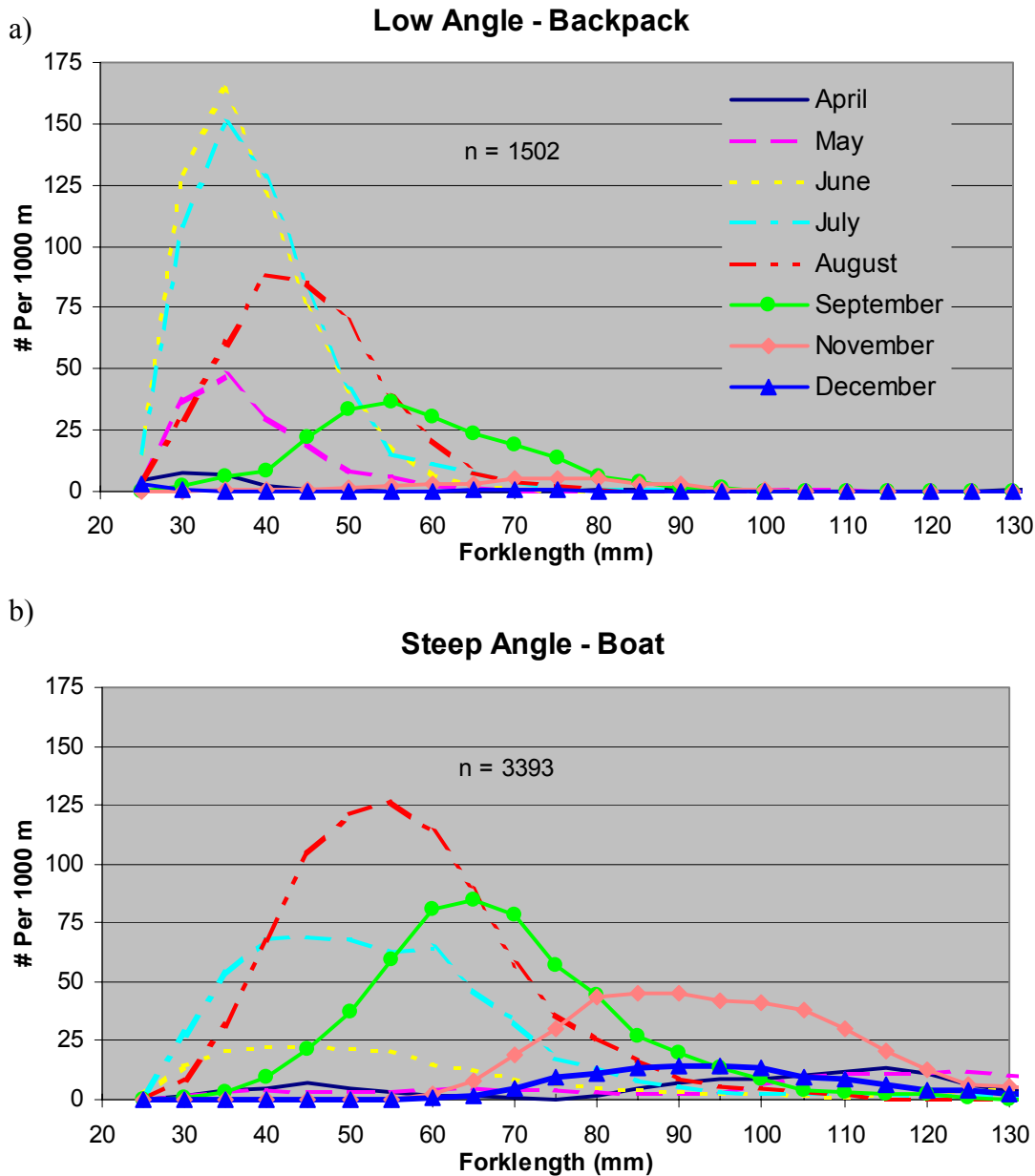


Figure 4.3. Length frequencies of YoY rainbow trout in Glen Canyon in a) low and b) steep angle habitats in 2004 by sampling trip. Sampling was typically completed in the first 5-10 days of each month (see Fig. 1.2 for sampling dates). Catches per 5 mm forklength category were smoothed using a 3-interval moving average for clarity of presentation.

increases as densities in low angle habitats increase, or alternately, that a higher proportion of newly emerged fish move directly to steeper habitats after emergence when densities in preferred low angle habitats are high. The number of YoY in steep habitats decreased in between the August, September, and November samples and size increased over this period. The density of YoYs in the December sample, taken shortly after the 42.5 kcfs Beach Habitat-Building Flow (Fig. 1.2), was much lower than in the previous months.

There were large numbers of fish in the 60-80 mm range in steep habitats in July while there were very few in low angle habitats at this time (Fig. 4.3). A likely interpretation is that most fish in this size range are moving from low to steep angle habitats. Note that low angle habitats are capable of supporting fish in the 60-80 mm range as evidenced by the September length frequency. Thus, movement of 60-80 mm fish from low to steep angle habitats may be dependent on density. Movement appears to be highest during the June and July period when the density of YoY is highest in low angle habitats and lowest in steeper habitats. As the season progresses, recruitment, movement, and mortality result in reduced densities in low angle habitats and increased densities in steeper ones. This may reduce the movement of fish from low to steep habitats as evidenced by the right-hand tail of the September length frequency. Interpretations of seasonal changes in length frequency by habitat type are challenging because they are influenced by a number of factors including seasonal patterns in recruitment to the sampling gear, growth, mortality, movement, and differential size- and habitat-based vulnerability to capture. The stock synthesis model presented in section 5.0 was very helpful in untangling these effects.

Length frequencies in low angle habitats in 2003 (Fig. 4.4) and 2004 (Fig. 4.3) show some common characteristics and some marked differences. Peak abundances of small YoY in both years occurred in late-June/early-July and there was a reasonable similarity in the decrease in numbers and increase in size across sampling trips. There was large decrease in density between late-July and early-September in 2003 relative to 2004. This decrease may have been caused by the sudden reduction in the daily minimum

flow from 10 to 5 kcfs at the beginning of September (Fig. 1.2). Interestingly, in 2003 these low angle habitats appear to have been recolonized by the October sample trip (Fig. 4.4). The magnitude and timing of the change in the minimum flow was identical in 2004, yet the decrease in density between early-August and early-September sample periods was much less than observed in 2003.

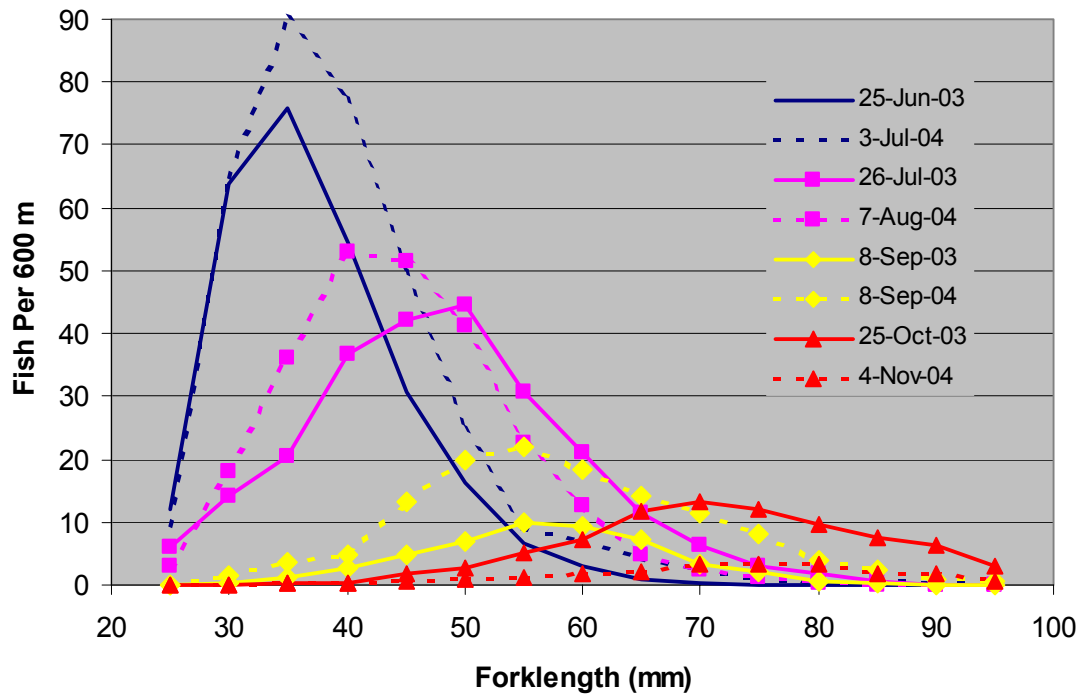


Figure 4.4. Comparison of length frequency samples from low angle habitats between 2003 and 2004. Lines with the same color and pattern represent sampling periods that were within 1-2 weeks apart between years.

4.2.2 Analysis of Otolith Microstructure

The otoliths from 260 YoY rainbow trout captured in 2003 were extracted and successful age determinations were made for 237 of these fish. In 2004, successful age determinations were made for 318 fish out of a total of 334. Age determinations were not possible for some fish due to difficulties encountered during preparation (otolith cracking or chipping) or for larger fish where counting increments became difficult to distinguish.

Age estimation in fish > 50 mm of length was noticeably more difficult than for smaller fish and fish >80 mm were very difficult to age reliably. For that reason, some ages for larger fish were not obtained, and replicate age estimates for larger fish were more variable than those for smaller fish. In contrast, the precision of otolith radius measurements was unaffected by fish size.

Hatch checks were clearly evident on all otoliths (Fig. 4.5). Emergence checks tended to be subtler and could not always be identified, thus age was determined relative to the hatch date. A major white band was observed in more than half of the total number of otoliths examined. The white band was often characterized by narrowing growth increments of low visual contrast, which increased in width and contrast immediately distal to the band. A prominent check was often, but not always, associated with the band. The band was present in all collection months, but was usually seen only in fish above 30 mm in length. Bands near the edge of the otolith were difficult to identify because of their position. The position and age of formation of the band was measured in 55 and 112 fish in 2003 and 2004, respectively. The age from hatch at which the white band was formed averaged 39 days (95% confidence limit of ± 16 days) in 2003 and 44 days (± 30 days) in 2004. Differences in the age of white check formation were not significantly different between years and were highly variable. The average size of fish at the time the major white-band was formed, determined from length back-calculation using the best-fit logistic length-age relationships, was 24-26 mm. The width of the band averaged 3-10 days. In Glen Canyon, fish between 25 and 28 mm often showed remnants of a yolk sac. Rainbow trout require 2-6 weeks to emerge following hatch (Moyle 2002, McEwan and Jackson 1996). The average number of days between hatch and the formation of the major white band corresponds to the upper-end of emergence time requirements from the literature. The white band likely represents the transition period between yolk-sac absorption and first-feeding.

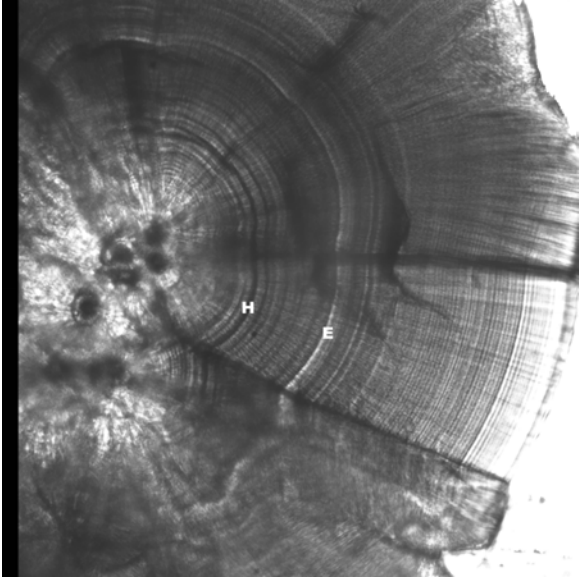


Figure 4.5. Magnified image (16x) of an otolith from a YoY rainbow trout captured in Glen Canyon in September, 2003 showing emergence (E) and hatch (H) checks. Each pair of dark and light rings represents one day of growth.

There was little error in the estimation of days from hatch based on a blind-test using hatchery fish of known age (Fig. 4.6). The estimated age of hatchery fish averaging 28 mm ($n = 11$) in length sampled 31 days after hatch on Jul. 24, 2003 ranged from 30-36 days with an average of 32 days. The estimated age from hatch for fish averaging 52 mm in length ($n = 10$) sampled 84 days after hatch on Sep. 15, 2003 ranged from 73-89 days with an average of 82 days. The precision of the daily age from hatch was ca. ± 7 days for larger fish and ± 2 days for smaller fish.

A weekly striping pattern (Fig. 4.7) was evident in at least 51% (131) of the 255 otoliths that were examined in 2003. A striping pattern was only evident on 20 of the 334 (5%) otoliths that were examined in 2004. Eighty-five percent of the fish with a striping pattern in 2004 were caught in April and May while in 2003 striping was observed in fish captured in all months. In general, striping was most evident in the middle and outer sections of the otolith, and in larger individuals. As the striping pattern was only obvious when several consecutive cycles were present, it is probable that additional otoliths from smaller fish had the pattern, but could not be identified. The atypical increment formed

every 7 days tended to be 25% wider (3.12 microns) compared to the other increments (2.51 microns) when averaged across all striping cycles from 15 fish, and the difference was statistically significant (Table 4.4). Within fish, the average increment width for the atypical bands was larger than the average width of the other increments in 14 of 15 cases, and the differences were often statistically significant when sample size for atypical increments was adequate.

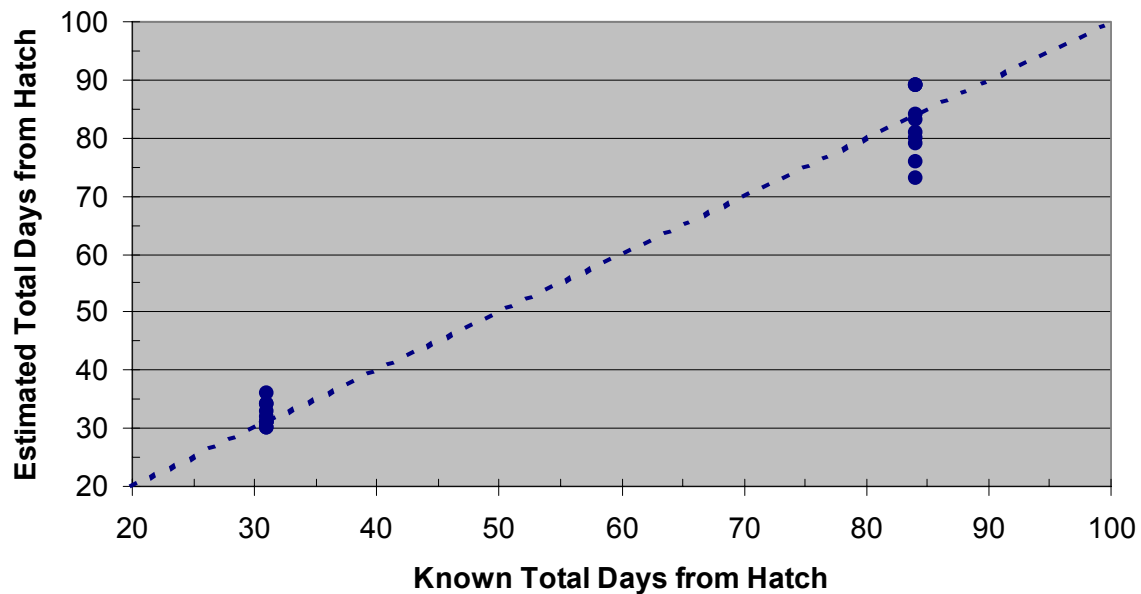


Figure 4.6. Comparison of estimated and known young-of-year age-from-hatch for wild rainbow trout that were spawned in a hatchery and sampled 31 and 84 days after hatching.

a)



b)

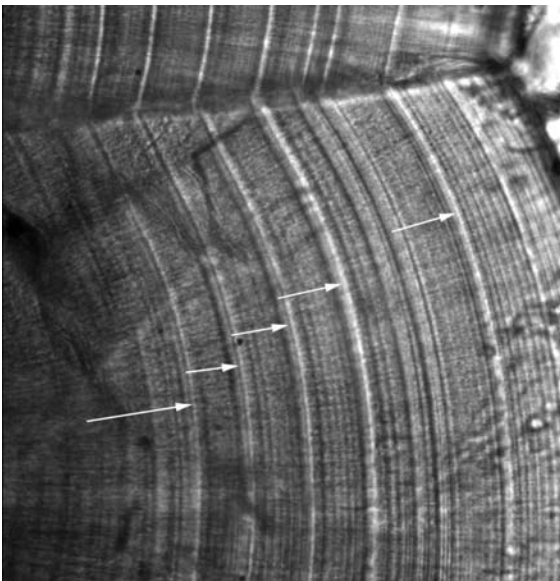


Figure 4.7. Images of a YoY rainbow trout otolith from Glen Canyon sampled in April 2003 showing a weekly striping pattern (identified by white arrows) at magnifications of a) 16x and b) 400x.

Table 4.4. Summary statistics for increment widths on otoliths from a sample of 15 fish where a weekly striping pattern was evident. The last column is the probability that differences in the width of typical and atypical increments is due to chance alone (e.g. Type I error rate).

Fish	# of Increments Measured		Average Width of Increments (microns)		Width Comparison Atypical > Typical	Probability
	Atypical	Typical	Atypical	Typical		
All 15	38	227	3.12	2.51	Yes	0.000
1	1	6	2.55	2.35	Yes	0.998
2	5	30	2.17	2.17		
3	2	12	3.03	2.77	Yes	
4	4	24	2.37	2.18	Yes	0.219
5	3	18	2.60	2.10	Yes	0.167
6	5	30	2.73	2.38	Yes	0.030
7	4	24	2.58	2.36	Yes	0.455
8	2	12	3.72	3.00	Yes	0.003
9	3	18	4.03	2.75	Yes	0.000
10	2	12	5.00	3.01	Yes	0.287
11	1	6	4.13	2.39	Yes	0.058
12	2	12	4.68	3.69	Yes	
13	3	17	4.31	2.78	Yes	
14	1	6	2.31	2.10	Yes	0.092
15	1	6	2.98	2.83	Yes	

The weekly striping pattern was very likely caused by the daytime Sunday steady flow regime. The periodicity of striping was exactly 7 days and corresponds with the weekly timing of Sunday steady flows. We know of no other physical event that occurred with a periodicity of exactly 7 days. We saw a much higher occurrence of striping in 2003 compared to 2004, which was likely caused by the differences in the Sunday flow regime across years (Fig. 4.8). Of those fish that did exhibit striping in 2004, the vast majority (85%) hatched during the early spring and were present when flows were relatively stable during the daytime on Sunday (+/- 3 kcfs in April and May). In comparison, the majority of fish which hatched later in the year were only exposed to

Sunday flows during the summer which were not that different from normal weekday operations.

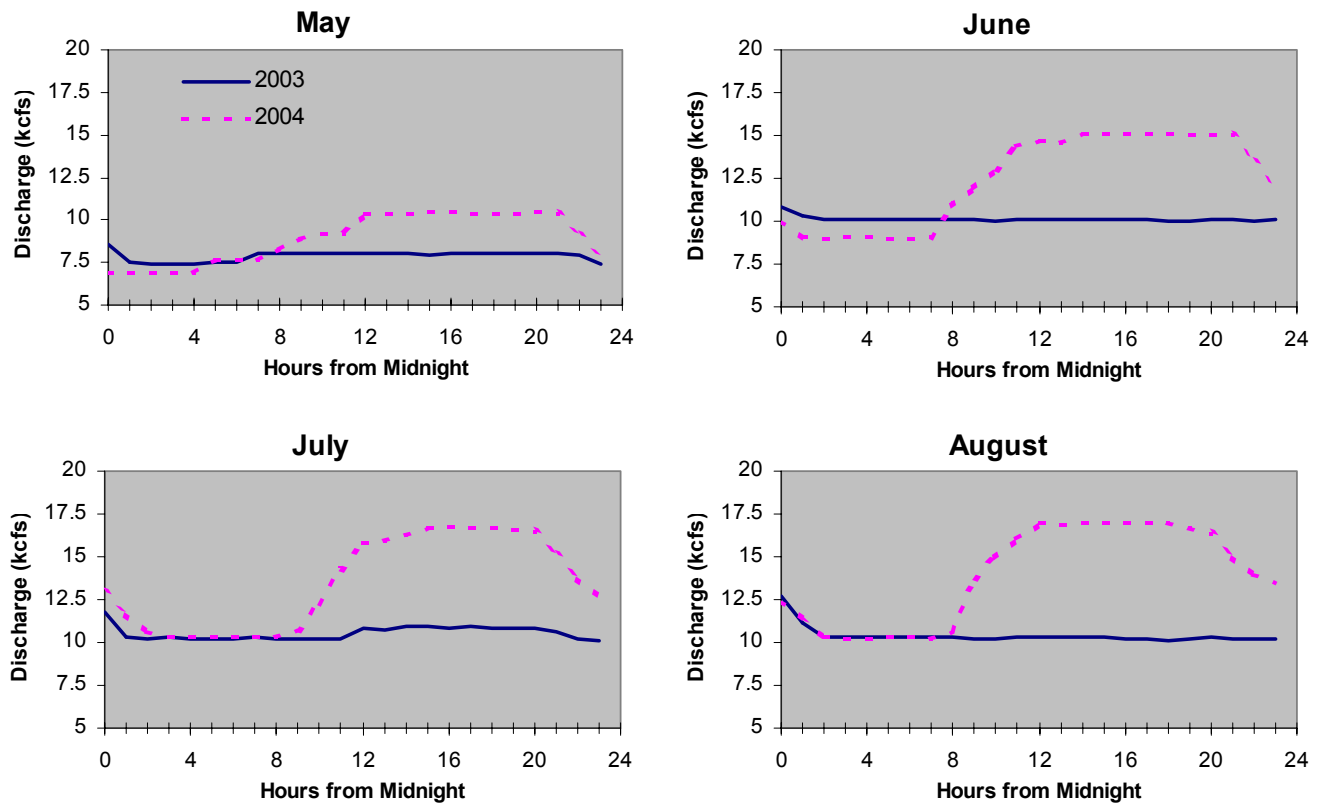


Figure 4.8. Comparison of 24-hr. typical hourly discharge patterns from Glen Canyon Dam on Sunday during the summer of 2003 and 2004. Discharge values are the average for that hour across all Sundays in the month.

Relationships between length and age for YoY rainbow trout in Glen Canyon were very strong (Fig. 4.9). The logistic growth model (eqn. 4.1) predicted 87% of the variation in forklength as a function of the number of days from hatch in 2003 and ($n=237$, $L_{\infty}=89.7245$, $K=0.0177$, $t_0=88.6944$) and 86% of the variation in 2004 ($n=318$, $L_{\infty}=92.2570$, $K=0.0216$, $t_0=91.7679$). The coefficient of variation (CV) in length-at-age based on 1-month age categories ranged from 7-21% with an average of 13% based on the 2004 data. When the analysis was repeated based on 1-week age categories the CV of length-at-age remained at 13%. Variation in length-at-age based on the 2003 data binned

into 1-month age categories ranged from 7-15% and averaged 12%. Size-at-hatch predicted by the most likely logistic growth models was 15 and 11 mm in 2003 and 2004, respectively. Size-at-hatch was also predicted by back-calculation. There were very strong linear relationships between the forklength and the length of the longitudinal otoliths axis from hatch to the edge of the otoliths (2003: $n=235$, $r^2=0.90$; 2004: $n=310$, $r^2=0.83$) and axis length and age-from-hatch (2003: $n=235$, $r^2=0.86$; 2004: $n=310$, $r^2=0.82$). The intercept of the axis length-age relationship provides an estimate of the axis length at hatch (2003: 59 μm ; 2004: 20 μm). Substituting these values into the forklength – axis length relationship resulted in back-calculated lengths at hatch of 15 mm in 2003 and 16 mm in 2004. These values were either identical or very close to those predicted by the most likely logistic models.

The logistic model predicting size at age using data combined across both years (Fig. 4.10) explained 86% of the variation in size ($n=555$, $L_{\infty}=93.5089$, $K=0.0189$, $t_0=92.9584$). The 2004 observed lengths-at-age were on average 0.5 mm above the predictions based on the most likely multi-year logistic model (combined 2003 + 2004 data) while the 2003 observed lengths were 0.65 mm below the predicted values. This provides weak evidence of differences in length-at-age among years which could be caused by real differences in growth rates or by changes in the sampling strategy. The most likely logistic length-at-age model based on data from steep habitats (2004 only) tended to predict that fish were slightly larger at a given age than the model based on data from low angle habitats (Fig. 4.11; Low: $n=120$, $r^2=86\%$, $L_{\infty}=88.6200$, $K=0.0123$, $t_0=92.0129$; Steep: $n=198$, $r^2=85\%$, $L_{\infty}=91.6318$, $K=0.02340$, $t_0=88.9764$). Differences in length-at-age were most pronounced for fish that were at least 3 months old and were statistically significant for fish 3-4, 4-5, and > 6 months old (Table 4.5). The most likely logistic model fit to the 2003 data, which was comprised of fish almost exclusively from low angle habitats, was virtually identical to the 2004 curve for low angle habitats. This suggests that differences in length-at-age in 2003 and 2004 (Fig. 4.10) were probably caused by including a large sample of fish from steep habitat types in 2004 (Fig. 4.11). There are two possible explanations why length-at-age for YoY in steeper habitats is larger: 1) growth rates for fish in steeper habitats tend to be slightly higher than those in

lower angle habitats; or 2) growth rates among habitat types are not different, but faster growing fish have a higher probability of colonizing steeper habitats.

Table 4.5. Comparison of mean length-at-age (mm) stratified by age (months from hatch) and habitat type. The last column is the probability that the difference in length-at-age between habitat types is due to chance alone (Type I error rate).

Months from Hatch	Number of Fish	Low Angle	Steep Angle	Probability
1-2	28	27	28	0.247
2-3	74	36	38	0.081
3-4	76	50	54	0.013
4-5	59	61	69	0.003
5-6	42	73	77	0.267
>6	33	76	85	0.021

The most likely length-at-age models for 2003 and 2004 were used to determine the date of hatch for each fish that was captured which were in turn used to develop hatch date distributions (Fig. 4.12). Hatch date distributions in 2003 (n=966) and 2004 (n=4647) were very similar and almost identical at the descending limbs. The majority of hatching in both years occurred between early February and late June. Differences in the ascending limb between 2003 and 2004 could be due to a higher proportion of early-season spawning in 2004, higher mortality of eggs and larvae for early-season cohorts in 2003, or differences in the timing of fry sampling among years. The first hypothesis of differences in the spawn timing of early-season fish can be ruled out as redd counts early in the season were very similar in 2003 and 2004 (Fig. 2.4). With regards to the third hypothesis, it is well established that the timing of sample collection can cause instability in back-calculated hatch date distributions. Given natural mortality, representatives of fish hatched early in the season will experience greater cumulative mortality than those hatched later. If sampling is not conducted throughout the hatching period, or the period when newly hatched fish are first vulnerable to capture, early season larvae will be underrepresented in the back-calculated hatch date distribution relative to late-season larvae (Campana and Jones 1992). It is unlikely that the 2004 hatch date distribution

shows such instability as our first sampling session in April occurred before virtually any newly hatched fish were vulnerable to capture (Fig. 4.3). However, the first substantive sample of YoY in 2003 occurred in late-June so differences in the ascending limbs of the 2003 and 2004 hatch date distributions could be caused by differences in sample timing. We generated an alternate 2004 hatch date distribution using a sample period that was consistent with 2003 by excluding the April, May, early June, and December samples. The modified 2004 hatch date distribution (n=3703) was virtually identical in shape to the one for 2003, suggesting the 2003 distribution underestimates the early hatch component and that between-year differences were caused by not sampling early enough in 2003.

We compared the back-calculated hatch date distribution for 2004 based on fry data with hatch date distributions estimated by redd counts. The date of each redd survey was increased by 33 days based on a requirement of 329 accumulated thermal units (Section 2) and an average water temperature over the incubation period of 10 C (Fig. 2.9). The correspondence in hatch date distributions from fry and redd count data was very strong (Fig. 4.13). We also compared the fry-based hatch date distribution with the prediction of the seasonal trend in the number of redds that would produce viable larvae based on their hypsometry and intergravel water temperatures (Section 2.2, Fig. 2.11a). As above, the date of spawning was advanced by 33 days. Note that the two redd-based distributions are not completely independent as the number of redds counted over the season is used as input to the model that predicts the number of those redds that will produce viable young. However, the latter indicator incorporates additional information used to predict incubation mortality. The correspondence between the fry back-calculated and egg mortality model-based hatch date distributions was again very strong. The peak of the fry back-calculated distribution was higher than that from the egg mortality model. Assuming the fry back-calculated hatch date distribution is correct, the egg mortality model appears to have underestimated the amount of spawning in mid-march, perhaps due to a greater amount of redd superimposition during the peak of spawning, and/or overestimated the amount of spawning or incubation survival after March 31st (there is no

spike in fry hatched on this date based on the back-calculation as the egg mortality model predicts).

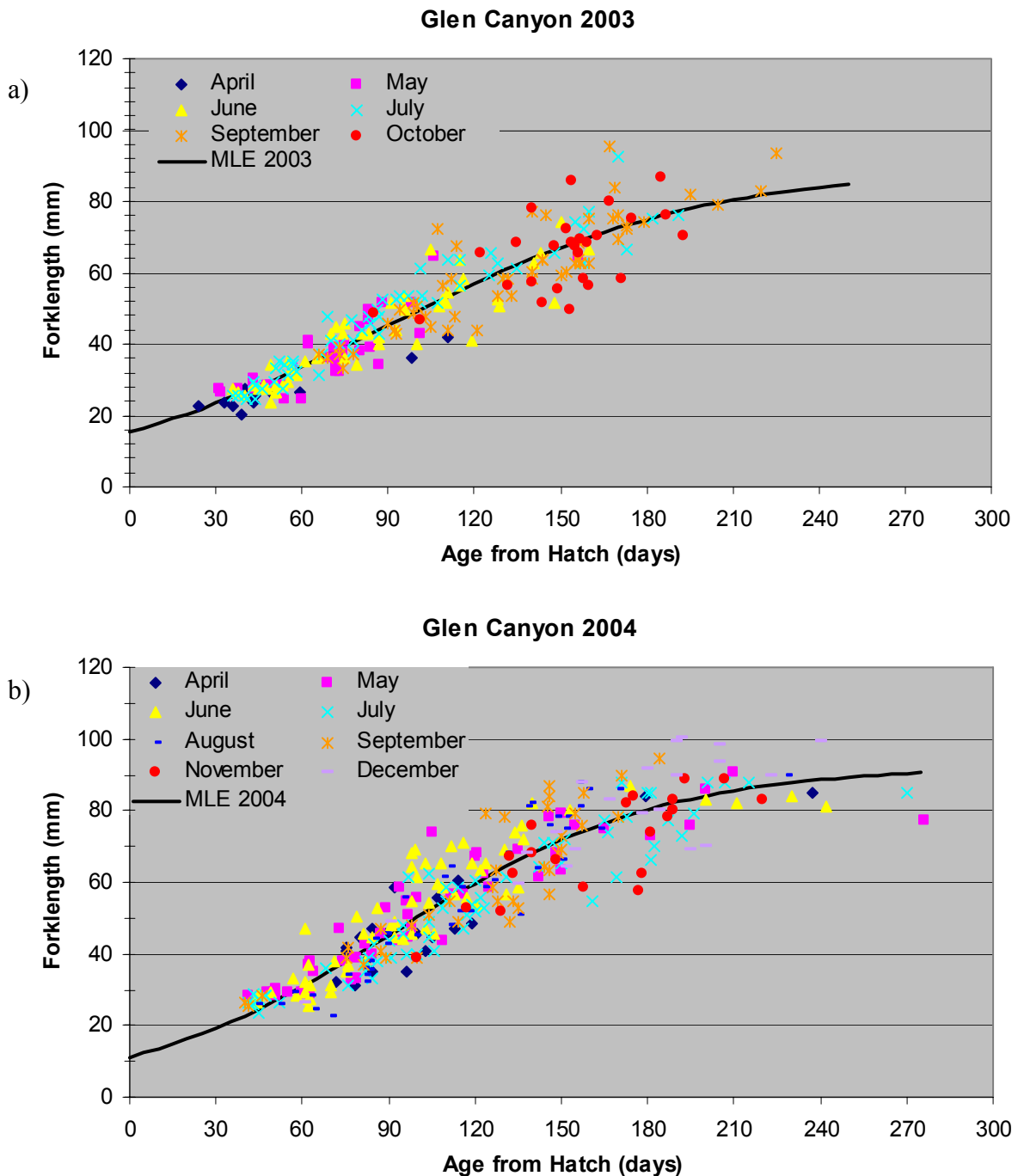


Figure 4.9. Length-at-age for YoY rainbow trout in Glen Canyon in a) 2003 and b) 2004. Data are stratified by month of sampling. Most likely estimates (MLE) for logistic growth models are also shown.

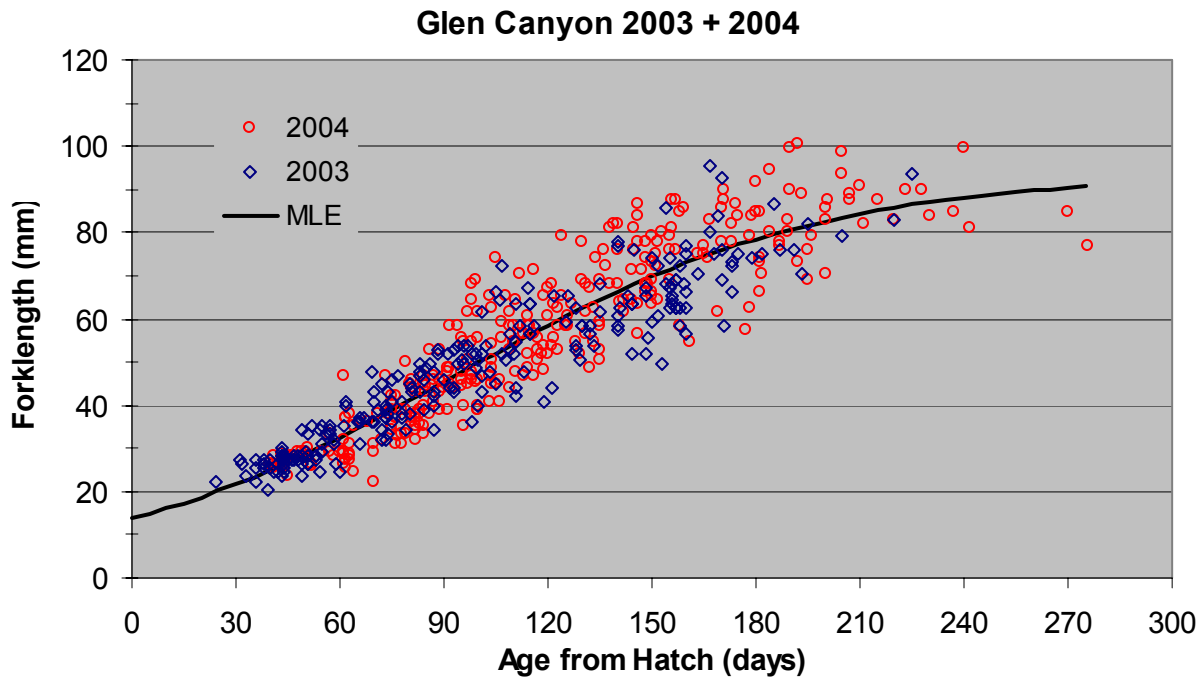


Figure 4.10. Combined length-age data from Glen Canyon in 2003 and 2004 and most likely estimate (MLE) of the logistic length-at-age model fit to all the data.

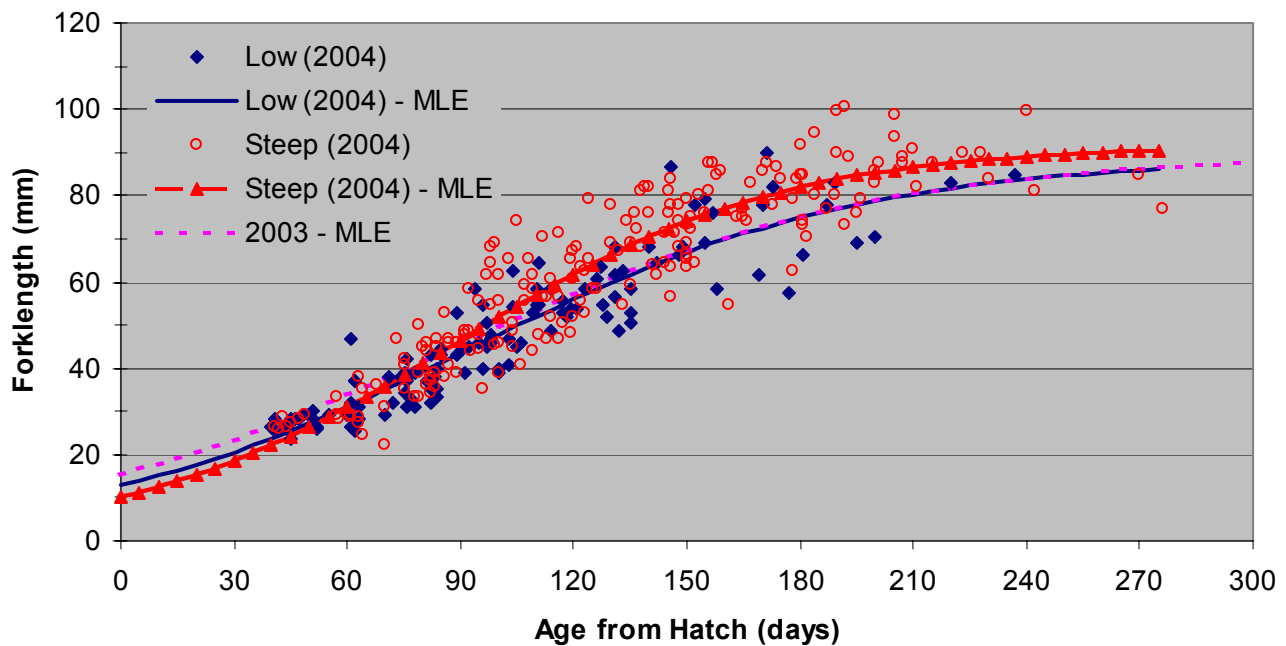


Figure 4.11. Length-at-age for Glen Canyon YoY rainbow trout sampled in 2004 stratified by habitat type and most likely estimates (MLE) for logistic models. Also shown is the most likely logistic model from 2003 that was based on fish sampled in low angle habitats only.

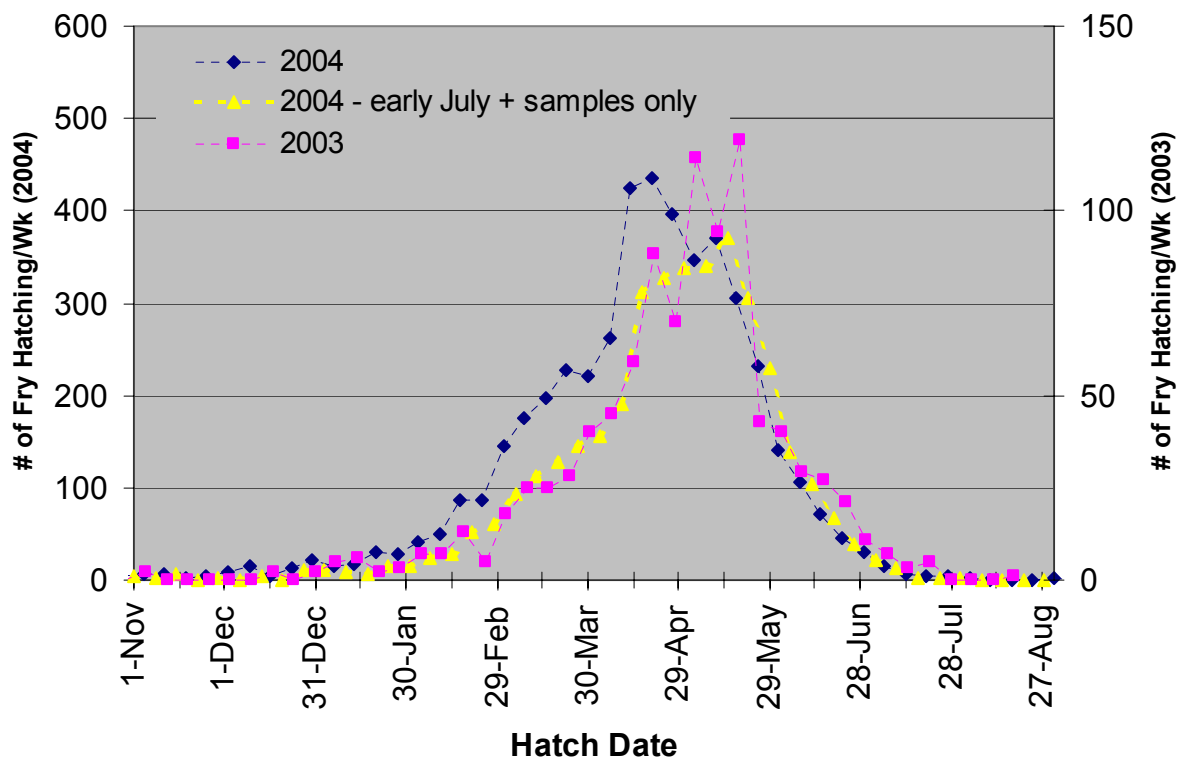


Figure 4.12. Predicted hatch date distributions of rainbow trout in Glen Canyon in 2003 and 2004. For comparison, the 2004 hatch date distribution based on data collected over a similar period to that in 2003 (2004 – July through December samples only) is also shown.

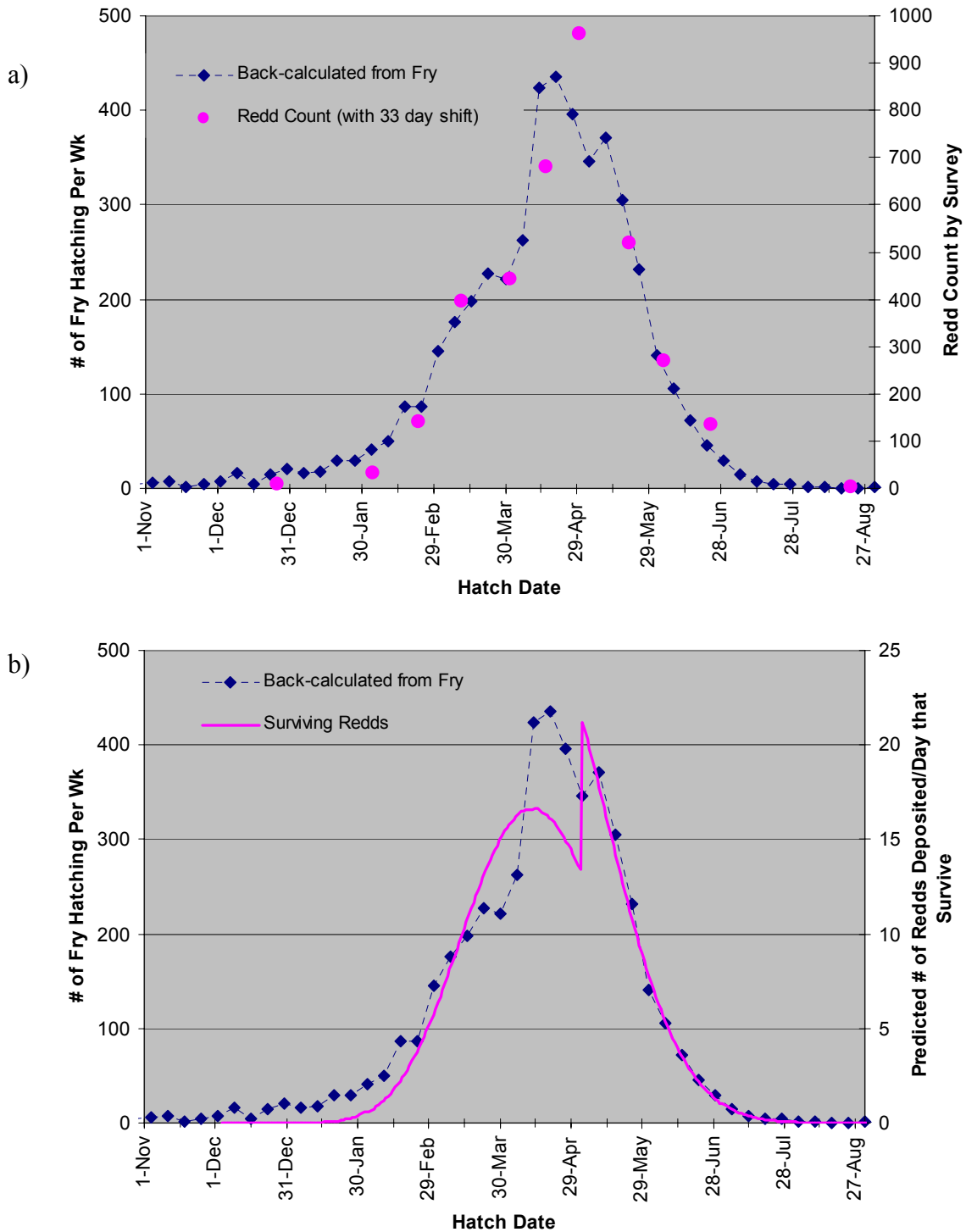


Figure 4.13. Comparison of hatch date distributions based on 3 methods: a) compares the hatch date distribution from fry whose ages were back-calculated from forklength with the expected distribution from redd counts (based on a 33 day shift to account the amount of time required between spawning and hatch); b) compares the back-calculated hatch date from fry with the expected distribution based on the number of redds predicted to survive from the egg mortality model (with a 33 day shift).

4.3 Conclusions from Analysis of Young-of-Year Data

Very small fish typically use nearshore areas where velocities are low enough for them to hold position and where depths are shallow enough to reduce predation risk from larger fish (Scott and Crossman 1973, Walters and Martell 2004). The basis for physical habitat models such as the Physical Habitat Simulation Model (PHABSIM), that predict how fish can be expected to respond to changes in river discharge, is that specific life stages of fish prefer microhabitats with specific characteristics and redistribute themselves as conditions change (Kemp et al. 2003). Thus, one would predict that YoY rainbow trout in Glen Canyon should follow the waters edge as it rises and falls on a diurnal basis to maintain preferred low velocity and shallow microhabitat. Our data show just the opposite. Catch rates were 3- to 5-fold higher when we sampled at the daily minimum flow compared to samples collected at the daily maximum. From this observation we hypothesize that the majority of YoY fish do not follow the waters edge as discharge rises over the day but are instead holding their position near the minimum flow elevation. Berlan et al. (2004) tracked the location of radio-tagged Atlantic salmon parr (mean size of 120 mm forklength) in a regulated river with diel fluctuations in discharge. They found that the parr occupied home ranges that were continually wetted; an observation consistent with our hypotheses that the majority of young-of-year do not follow the waters edge as it rises but instead remain over permanently wetted habitat. Our hypothesis is also consistent with other studies that show that young-of-year are reluctant to shift their lateral position in response to sudden increases in flow (Shirvell 1994, Vehenan et al. 2000). An alternative hypothesis explaining the differences in density we observed is that catchability could have been higher at the minimum daily discharge relative to the maximum. Because sampling was restricted to the nearest 2.5 m from shore, differences in physical conditions that could affect catchability, such as depth and velocity, were very minor between minimum and maximum daily flows (Table 4.3). Differences in catch rates at maximum and minimum daily discharges were consistent across samples taken at night and during the day where potentially large differences in catchability would be expected. It therefore seems unlikely that differences in catchability

between maximum and minimum flows could explain the large differences in densities that were observed.

The weekly striping pattern observed on the otoliths that we examined is perhaps indicative of the very risk adverse behaviour of young fish. During 2003, otolith daily increment width, an index of growth rate, was 25% higher on Sundays when daytime flows were held steady at levels near the minimum daily flows that occurred over the rest of the week. The evidence that these stripes were caused by Sunday steady flows was irrefutable: the striping pattern occurred with a periodicity of exactly 7 days and was only evident when Sunday steady flows were implemented, which occurred throughout the post-emergent period in 2003 and only the beginning of the post-emergent period in 2004. The maximum vs. minimum daily flow catch rate comparison demonstrates that YoY are likely holding at the minimum flow elevation when discharge is high during the week and on Saturday. The Sunday-weekday growth differences suggest that this behaviour must either increase energy expenditure, limit daily ration, or both. Foraging arena theory predicts that juvenile fish will attempt to maximize their growth rate while at the same time minimize their probability of being eaten (Walters and Martell 2004, Walters and Korman 1999). In Glen Canyon it appears that on a diel time-scale, the increased predation risk caused by moving with the waters edge to obtain more suitable foraging/resting conditions is not worth the energetic benefits.

Reluctance of YoY fish to immediately respond to micro-scale changes in depth is almost certainly the reason why young fish are stranded during sudden or unusual flow reductions. The extent of stranding has been shown to be highest in low-angle habitats with abundant cover (Halleraker et al. 2003) such as the low angle *Cladophora* covered-cobble bars and macrophyte-covered sand bars of Glen Canyon. It is possible that the decrease in YoY densities observed in low angle habitats in the September sample was the result of fish stranding due to a change in the minimum daily flow from 10 to 5 kcfs. Alternately, the flow change may have caused fish to move to another habitat type or location that was not sampled, but foraging arena theory (Walters and Korman 1999) suggests that there would likely be an increased mortality risk associated with doing so.

The diel behaviour and post-September density changes we have documented in Glen Canyon, coupled with the substantial literature on stranding impacts, support implementation of an experiment to test the feasibility of regulating YoY recruitment through implementation of a 'stranding' flow operation from GCD. Ideally, a high steady flow of 15-20 kcfs would be maintained for a few days to force YoY fish to migrate to the high elevation-waters edge. The high flow would be followed by a sudden reduction to 5-8 kcfs with an unrestricted ramp rate. A system wide estimate of fry density before and after the flow reduction would document the extent of the impact. By sampling both low and steep angle habitats we could determine whether the stranding resulted in substantial mortality or simply displaced fish. Sampling during the high flow increase would allow us to determine the length of time required for fish to move from the minimum daily flow elevation to the temporary elevation associated with the high flow. Sampling both low angle and steeper habitats would allow us to determine if fish residing in the latter habitat are less vulnerable to sudden flow reductions as we might expect. This would have relevance to evaluating potential unwanted impacts on other species, such as juvenile humpback chub, that make extensive use of talus shorelines (Converse et al. 1998). If substantial mortality of YoY rainbow trout is observed, long-term implementation might involve conducting the stranding flow two times per month from June through July when the majority of YoY are very small and occupying low angle habitats where stranding impacts would likely be most severe.

Implementation of a stranding-type operation should only be entertained if reducing YoY survival in Glen Canyon is consistent with management objectives. Reduced recruitment rates could result in a population size in Glen Canyon that is below the current management target of 100,000 fish > 150 mm. A smaller population could lead to an increase in the size of fish caught by anglers, but this benefit potentially conflicts with the current abundance target. If a significant number of rainbow trout from Glen Canyon disperse downstream into Marble Canyon, and if the dispersal rate were density-dependent, a reduction in the density of fish in Glen Canyon would help meet the management objective of reducing the abundance of rainbow trout in Marble Canyon.

Data on the trade-off between size and abundance of rainbow trout in Glen Canyon, and on the magnitude and dynamics of downstream dispersal would be very useful for determining whether flows targeted at reducing recruitment rates in Glen Canyon should be seriously considered.

Daily variation in discharge from 5-20 kcfs, which is beyond that specified in the ROD, has been implemented from January through March from 2003-2005. While this operation increases hydro power revenues, its original intent was to control rainbow trout recruitment to test whether this increases the survival of humpback chub juveniles. Our egg mortality estimates suggest that the impact of this operation on incubating stages of rainbow trout has been relatively minor compared to normal ROD operations and almost inconsequential relative to historic impacts when there was little natural reproduction (Section 2.0). Unfortunately, the sustained 20 kcfs flows during the January to March period has been shown to substantially increase the export rate of sand from Marble and Grand Canyons and promoted rapid bar erosion of new beaches deposited by a high-flow test in November 2004. Given this negative impact, and the likely ineffectiveness of the higher flow fluctuations for controlling trout recruitment, an alternate regime for the winter and spring of 2006 needs to be seriously considered.

Comparison of hatch date distributions from redd and fry surveys can be used as a means of monitoring egg and alevin survival in Glen Canyon. There was a very strong relationship between length and age-from-hatch for YoY rainbow trout. We used this relationship to compute the age of all fish that were captured and to determine their hatch date based on the date of capture. Hatch date distributions were very consistent between 2003 and 2004. The correspondence between the back-calculated hatch date distribution in 2004 and the one based on redd surveys was striking. This suggests that there were no large seasonal differences in egg and alevin mortality. The egg mortality model (Section 2) predicted a much higher mortality rate if Sunday daytime flows were reduced from 8 to 5 kcfs. If this operation was implemented say, for the latter half of the spawning period in mid-March through April, and redd and fry monitoring were continued, the hatch date distribution back-calculated from surviving fry should be well below that based on redd

counts for this same period. Such a comparison would provide much more certainty about the population-scale impacts of redd dewatering than our model-based estimates.

Differences in length frequencies over time and among habitat types showed the effects of size-based vulnerability, recruitment, growth, mortality, and ontogenetic habitat shifts. There is no debate that these processes exist, but there are few studies that document them so clearly in the field. However, addressing quantitative questions of relevance to management using the length-frequency data alone is difficult. For example, was the decline in numbers of YoY in low angle habitats between the August and September in 2004 a result of mortality or movement to steep angle habitats where catchability is different? Was the decrease in density between November and December 2004, in steep habitats expected based on the apparent mortality rates in previous months and the time between sampling periods, or was it higher, perhaps because of the high-flow test in late November? To address these questions we require a model that predicts seasonal changes in length frequencies among habitat types as a function of hatch timing, mortality, growth, and movement. As the length frequencies we observe are a biased sample of the true frequencies, we also need to account for size-dependent vulnerability and differences in vulnerability across habitat/gear types. In Section 5.0 we develop a model that accounts for these dynamics and apply it to the length frequency and length-at-age data to quantitatively address these and other questions.

5.0 Estimation of Hatch timing, Survival Rate, and Ontogenetic Habitat Shifts for Juvenile Salmonids Using a Stock Synthesis Model

Detecting changes in salmonid populations is not easy, and linking those changes to human-induced habitat alterations is even more challenging. The ultimate objective of almost all habitat restoration efforts is to increase the abundance of an adult population. It is well established that the strength of a year class or cohort is usually determined by the growth and survival of fish in their first year of life. With the exception of very short-lived species, there is usually a substantial delay between the time that a habitat change affects the survival rate of young fish and when that change potentially becomes detectable in the adult population. Furthermore, a difference in the success or failure of a single or a few adjacent cohorts may be difficult to observe in an adult population that is made up of multiple cohorts and where there is considerable variation in length-at-age or substantial error in age estimates. Monitoring the population response of juvenile fish to habitat changes therefore seems a logical alternative, or at least a necessary supplement, to monitoring adults. Monitoring the adult population provides a measurement of the variable that fisheries managers usually care most about. It also measures abundance after the majority of density-dependent processes have occurred, which potentially compensate for changes in morality due to habitat effects. Juvenile monitoring likely provides more precise measurement of habitat change that can be more readily linked to the imposed management action.

The impacts of flow regulation and other river restoration actions on juvenile salmonids can be divided into factors that affect the incubation environment for egg and alevin life stages, and those that change the availability and quality of fry and parr rearing habitat. The implementation of increased diurnal fluctuations in flow from Glen Canyon Dam from January through March of 2003-2005 was intended to destabilize nearshore habitat to reduce the survival rate of newly-emerged non-native salmonids. Our data showed that the timing of the increased fluctuations (Fig. 1.2) was too early to affect YoY rainbow trout (Fig. 4.12) and instead only had the potential to affect incubation mortality. We provided a model-based estimate of seasonal trends in incubation mortality

(Fig. 2.11) that needs to be verified through long-term monitoring under a range of dam operations. A simple examination of seasonal length frequency data showed possible impacts of specific dam operations on survival rates during the summer and fall, although it was difficult to untangle the confounding effects of size-dependent vulnerability, hatch timing, and normal ontogenetic habitat shifts (Fig. 4.3). From a long-term monitoring perspective, a more rigorous and quantitative assessment procedure, that provides a relative estimate of annual and seasonal changes in incubation and post-emergent survival rates would be very useful.

Statistical catch-at-age or stock synthesis models are commonly used in major fish stock assessments (Hilborn and Walters 1992). These models combine information on trends in relative abundance from catch or scientific surveys with information on size and/or age composition to estimate recruitment to the vulnerable population and natural and fishing mortality rates (Walters and Martell 2004). A plot of the number of fish by age based on a single sample, or catch-curve, is influenced by the combined effect of age- or size-dependent differences in vulnerability, recruitment (population growth or decline causing an over- or under-representation of younger fish in the catch-curve), and mortality. It becomes possible to untangle these effects when catch-curves from multiple years are analyzed together (e.g., Pauly et al. 1987). However, there is generally large uncertainty in recruitment and survival rate estimates in most assessments because there is: 1) an insufficient number of catch-at-age samples spread out over time relative to the lifespan of the fish; 2) considerable natural or ageing error-induced variation in length-at-age; and 3) substantial changes in vulnerability over time due to changes in fishing effort or the spatial/temporal distribution of the vulnerable population.

In this analysis, we combine length-at-age and length-frequency data from Glen Canyon in 2004, in a stock synthesis model to estimate hatch timing and ontogenetic movement and survival rates for YoY rainbow trout. The model we developed is similar to the ones used in fish stock assessments except it tracks the abundance of weekly cohorts of fish for one year from the time of hatching, rather than annual cohorts over multiple years. Our application of this stock synthesis model avoids the main pitfalls in

most stock synthesis assessments. First, we obtained eight length frequency samples on a monthly basis that was helpful to partially untangle recruitment and survival rate effects. Second, we obtained a large length-stratified age sample for young fish, which show relatively little variation in length-at-age. Finally, we maintained a very consistent fishing protocol in two habitat types throughout the sampling period, helping to minimize problems associated with changes in vulnerability resulting from changes in fishing effort or from changes in habitat use as fish grow.

In this analysis, the stock synthesis model is used to address three questions of direct relevance to flow management targeted at controlling rainbow trout recruitment and survival in the Colorado River below Glen Canyon Dam. First, we evaluate the ability of the model to estimate the apparent annual survival rate for fish in their first year of life as a long-term monitoring metric. Second, we compare the weekly pattern in the relative number of hatching fish with those expected from repeated redd counts to evaluate the possibility of using the model, in conjunction with redd surveys to derive a reach-wide annual index of incubation success. Finally, we evaluate the model's ability to estimate changes in the apparent survival rate within a year. We saw evidence of reduced abundance following the reduction in the daily minimum flow in early-September and following the Beach Habitat-Building Flow test in late-November 2004. We use the model to help untangle movement, catchability, and vulnerability effects in the length frequency data that confound our ability to assess potential changes in survival rate caused by these flow changes. The model is fit to the data using maximum likelihood which allows us evaluate the statistical significance of differences in survival rates across these major flow events. Model structure, most likely parameter estimates, and uncertainty are described for a range of models of increasing complexity. The benefits and weaknesses of the proposed juvenile monitoring methodology are discussed. A detailed description of data collection methods and the data used to parameterize and fit the model is provided in Section 4.0.

5.1 Stock Synthesis Modelling Methods

The model tracks the number of fish alive from weekly cohorts in low and steep angle habitats for a 1-year period beginning January 1st on a weekly time-step. Recruitment in this analysis represents the total number of fish hatching in Glen Canyon. The model accounts for length-based differences in survival rates and allows for different survival rates among habitat types and between sampling periods. Movement from low to steep angle habitats is predicted as a function of fish length and density in low angle habitats. The number of fish alive at each age is translated into a length frequency based on a length-at-age key that accounts for variation in length-at-age and a length-based vulnerability function. Model parameters are estimated by fitting the model to the observed length-frequency data using maximum likelihood.

The number of fish that hatch and recruit to the population at age 0 on week t ($N_{0,t}$) is predicted using the beta distribution,

$$(5.1) \quad N_{0,t} = R \int_{t-1}^t \theta_t^{(\alpha-1)} (1 - \theta_t)^{(\beta-1)} dt,$$

where R is the total recruitment over the simulation period and α and β are parameters of the beta distribution that define the timing of hatch. θ_t represents the proportional date of hatch and ranges from 1/52 on the first possible week of hatch (beginning on Jan. 1) to 1 on the last week T . The use of a beta distribution assumes that recruitment timing follows a smooth function where the recruitment in one week is correlated with values in the previous and following weeks. We also allowed $N_{0,t}$ to be predicted independently for each week by replacing eqn. 5.1 with $N_{0,t} = Rr_t$, where r_t is the proportion of the total recruitment produced on each week of the simulation.

The number of YoY alive on week t of age a in low angle habitat type L ($N_{L,a,t}$) is predicted from,

$$(5.2) \quad N_{L,a,t} = N_{L,a-1,t-1} (1 - \text{MOV}_a) S_L,$$

where MOV_a is the proportion of fish of age a that move from low angle to steep habitats, and S_L is the weekly survival rate in low angle habitat. S_L can vary between sampling periods or can be held constant for the entire simulation. MOV_a is estimated using a logistic function relating the proportion of fish moving to forklength,

$$(5.3) \quad \text{MOV}_a = \frac{l^{\text{MovSl}}}{\text{MovHalf}^{\text{MovSl}} + l^{\text{MovSl}}},$$

where l is the mean forklength at age a , MovHalf is the forklength at which the proportion of fish in low angle habitat moving to steep habitat in one week is $\frac{1}{2}$ it's maximum value of 1.0, and MovSl is the slope of the relationship. The number of YoY alive in steep habitats is predicted from,

$$(5.4) \quad N_{S,a,t} = (N_{S,a-1,t-1} + N_{L,a-1,t-1} * \text{MOV}_a) * S_S,$$

where S_S is the weekly survival rate in steep habitat. As for S_L , S_S can vary between sampling periods or not.

To model age-specific differences in mortality we used the allometric relationship between natural mortality and body length of Lorenzen (2000),

$$(5.4) \quad M_l = M_r * \left(\frac{l}{l_r}\right)^c,$$

where M_l is the instantaneous mortality rate at forklength l , M_r is the mortality rate at reference forklength l_r , and c is the allometric exponent of the mortality-forklength relationship. We assumed that $c = -1$ following Lorenzen's (2000) analysis based on stocking experiments of salmonids of various sizes, Note that $c = 0$ can be used to simulate the case where mortality does not change with size ($M_r = M_l$). The reference

forklength was assumed to be 50 mm and M_r was estimated from the data after transforming S_L and S_S to instantaneous rates using $M = -\ln(S)$.

The mean length for a fish of age a was predicted using the logistic growth model,

$$(5.5) \quad L_a = \frac{L_\infty}{1 + e^{-K(a-t_0)}} + v_a ,$$

where L_a is the predicted forklength at age a , K is the instantaneous growth rate at the origin of the curve, L_∞ is the asymptotic length, t_0 is the age at the first inflection point of the curve which corresponds to the age of the maximum absolute growth rate, and v_a is a normally distributed error term reflecting the extent of variation in length-at-age with an age-specific standard deviation of σ_a (Campana and Jones 1992). A length-at-age key was created by determining the proportion of fish of age a in 5 mm length category l ($P_{l,a}$) using the equation,

$$(5.6) \quad P_{l,a} = N(l, L_a, \sigma_a) - N(l-5, L_a, \sigma_a) ,$$

where $N()$ is the cumulative normal distribution with mean length L and standard deviation σ . The number of fish alive in each habitat type h , 5 mm length category l , and week t ($N_{h,l,t}$) was computed as,

$$(5.7) \quad N_{h,l,t} = \sum_{a=1}^{a=T} P_{l,a} N_{h,a,t} ,$$

The number of fish in any length category therefore includes fish from multiple ages due to the simulated variation in size at age from eqn. 5.6.

The number of fish caught by size category in each habitat type ($C_{h,l,t}$) is predicted from,

$$(5.8) \quad C_{h,l,t} = N_{h,l,t} * q_h * V_{h,l} ,$$

where q_h is the catchability by habitat type and $V_{h,l}$ is a relative size-dependent vulnerability ranging from 0 to 1. Catchability represents the total proportion of YoY fish alive in the reach over the simulation period that are vulnerable to capture based on sampling 600 m of low angle shoreline (q_L) and 1000 m of steep angle shoreline (q_S) per trip. Relative vulnerability is predicted as a logistic function of forklength,

$$(5.9) \quad V_{h,l} = \frac{l^{VulSl_h}}{VulHalf_h^{VulSl_h} + l^{VulSl_h}} ,$$

where l is a 5 mm forklength category, $VulHalf_h$ is the forklength at which vulnerability is $\frac{1}{2}$ its maximum value of 1.0, and $VulSl_h$ is the slope of the function.

Hatch timing, vulnerability, movement, and survival rates were fit to the April-December 2004 length frequency data from Glen Canyon. We assumed the error in the model followed a Poisson distribution (Hilborn and Mangel 1997),

$$(5.10) \quad P(k_{l,t} | S_h, \alpha, \beta, VulHalf_h, VulSl_h, MovHalf, MovSl) = \frac{e^{-P_{l,t}N_t} (P_{l,t}N_t)^{k_{l,t}}}{k_{l,t}!} ,$$

This model computes the probability of the model parameters based on the observation of catching k fish in the each 5-mm length category l on week t . The total catch for the sample on week t (N_t) and the proportion of the total catch in length category l ($p_{l,t}$) in that week were predicted by the model as a function of the parameter estimates. A non-linear iterative search procedure was used to minimize the sum of the negative log-likelihoods of eqn. 5.10 across both habitat types and for all length categories and sample periods. The log-likelihood, $\ln(L)$, for a single habitat type, length category, and sample week is,

$$(5.11) \quad \ln(L) = -p_{l,t}N_t + k_{l,t}(\ln(p_{l,t}) + \ln(N_t)) ,$$

Four models of increasingly complexity were fit to the observed length-frequency data based on different assumptions regarding hatch-time and survival dynamics. The simplest model, where survival rate for a fish of age a is constant across all sample periods and where weekly recruitment (# of fish hatched) is predicted from a beta distribution, consists of 10 parameters (ConstSurv-BetaRec). Allowing survival rate to vary between the eight sample trips, that is, replacing S_h in eqn. 5.10 with seven survival terms per habitat type, increases the number of parameters to 22 (VarSurv-BetaRec). Allowing independent estimates of weekly recruitment by replacing the beta distribution in eqn. 5.1 with r_i up to the last sample period, coupled with a constant survival rate, results in 56 parameters (ConstSurv-WeekRec). The most complex model allows variation in survival rates among trips and independent weekly estimates of survival rate and has a total of 68 parameters (VarSurv-WeekRec).

We used a likelihood ratio test to evaluate the statistical reliability of increasingly complex models. Twice the difference between the log-likelihood values from two different models has a Chi-square distribution with the degrees of freedom equal to the difference in the number of parameters between models (Hilborn and Mangel 1997). A more complex model would be considered to be significantly better than a simpler model if twice the difference in log-likelihoods among models exceeded the threshold Chi-square value at the specified Type I error level (e.g., $\chi^2=1.94$ at a Type I error rate of 0.05). Uncertainty in parameter estimates was computed by systematically varying the parameter of interest and estimating the most-likely values for the other parameters using a non-linear search procedure. Negative log-likelihoods for each parameter value were converted to probabilities based on a likelihood ratio test with 1 degree of freedom.

Catchability (q_h) was calculated at its most-likely estimate for any parameter combination which is simply the ratio of the observed catch across all sample trips to the predicted catch per habitat type. On each sampling trip we sampled 2% and 5% of the total shoreline length of low and steep angle habitat in Glen Canyon, respectively. If all hatched fish that survived to an age when they were vulnerable,, were randomly

distributed among all potential sites, and if we caught all the fish present at each sampling location, maximum values of q_L and q_S would not exceed these percentages. To be conservative in our estimation, that is, to ensure we do not underestimate the uncertainty in parameter estimates, we doubled these proportions and set q_L and q_S to 0.05 and 0.10, respectively. We also examined parameter uncertainty at the unlikely, but most conservative catchability constraint possible, of $q_L=1$ and $q_S=1$.

We did not attempt to estimate the total recruitment of hatched fish (R in eqn. 5.1) as catchability was computed at its most likely value conditional on other parameter estimates. With this structure large estimates of total recruitment for a given survival rate would be absorbed by lower estimates of catchability, and visa-versa. We therefore set R to a realistic maximum value of 2,000,000 fish. We estimated that a total of approximately 2,000 redds were excavated in 2004, based on repeated redd surveys spanning the entire spawning period (Fig. 2.4a). Assuming 1,000 eggs/female, the low end of the fecundity range for rainbow trout in Glen Canyon (Maddux et al. 1987), one redd/female, and a 100% survival rate from fertilization to hatch, leads to the very optimistic prediction of 2,000,000 fish at hatch. Using a maximum value for the number of fish that successfully hatched minimizes the possibility that the catchability constraints would be binding at low survival rates. This in turn would provide the most conservative estimates of uncertainty. At very high survival rates the value of R is absorbed by the catchability calculation and would therefore have no effect on the likelihood of these rates.

Age from hatch was determined by counting daily rings on the sagittal otoliths of 318 fish collected from a length-stratified sample of the catch on each sampling trip (Section 4.1.2). Parameters for the logistic growth model (eqn. 5.5) were estimated by minimizing the sum of squares between predicted and observed lengths. The most likely model (Fig. 4.9b) predicted 86% of the variation in forklength as a function of the number of weeks from hatch ($n=318$, $L_\infty=92.26$, $K=0.022$, $t_0=91.77$). The coefficient of variation in length-at-age based on one-month age categories ranged from 0.07-0.21 with

an average of 0.13. The standard deviation used in the computation of the length-at-age key (eqn. 5.6) was calculated as $\sigma_a = 0.13 * L_a$.

5.2 Stock Synthesis Modelling Results

5.2.1 Comparison of Most-Likely Models

Estimates of weekly survival rate in both habitat types from the constant survival models were approximately 0.85 and were not dependent on the form of the recruitment distribution (Table 5.1). The models predicted knife-edge vulnerability at 29 mm in low angle habitats, and a more gradual length-vulnerability relationship in steep angle ones. These estimates are consistent with our intuition as we would expect to catch a higher proportion of very small fish by backpack electrofishing (used to sample low angle habitat) than by boat electrofishing (used to sample steep angle habitat). The most likely parameters from the movement-forklength relationship predicted moderate movement rates with only minor size effects. For example 7%, of fish that were 50 mm in length would move from low to steep angle habitats per week with an increase to 11% for fish 80 mm in length.

The constant survival rate models provided good fits to the length frequency data in low and steep angle habitats with some interesting exceptions. The abundance of 30-45 mm fish in low angle habitats was overestimated in May when weekly recruitment was predicted using the beta distribution (Fig. 5.1), but not when it was allowed to vary independently by week (Fig. 5.2). The beta distribution provided a very plausible fit to the likely true hatch timing derived by advancing the dates of redd counts to hatch dates based on measured intergravel water temperatures (Fig. 5.3). The beta distribution also provided a good fit to the hatch date distribution estimated by length back-calculation with no adjustment for differences in cumulative mortality between younger and older fish. Not surprisingly, the simpler two-parameter recruitment timing function was not able to capture the subtler variations in recruitment timing seen in the back-calculated hatch date distribution as well as the higher order model that allowed recruitment to vary

independently by week. In spite of the large increase in the number of parameters associated with estimating recruitment independently for each week, the model produced a statistically much better fit (Type I error probability <0.001) to the data than the one where weekly recruitment was predicted using a beta distribution.

The constant survival rate model substantially over-predicted the abundance of 40-55 mm fish in June in steep angle habitats regardless of the recruitment-timing model (Fig. 5.1 and 5.2). There was little difference in observed length frequencies between the June and July samples in low angle habitats but a four-fold increase in density over this period in steep habitats. If movement rates were proportional to density as assumed in our model, we would have expected a much higher abundance in steep habitats by early-June. A threshold density or sustained period of high densities in low angle habitats must therefore be required before substantial movement to steeper habitats is initiated.

In November 2004, the number of fish 100 mm and larger predicted by the model was much lower relative to the observed numbers. Our length-at-age relationship, derived mostly from samples obtained before November, likely underestimated growth rates during the late-Fall period. Mean daily water temperature increased from 10 to 14 C between early July and early November ([http:// www.gcmrc.gov/ what_we_do/ products/ discharge_temp/ discharge_temp.htm](http://www.gcmrc.gov/what_we_do/products/discharge_temp/discharge_temp.htm)). This change could have increased length-at-age by the 5 mm required to better fit the observed length distribution from November. However, note that the total number of fish > 80 mm in September was about $\frac{1}{2}$ the abundance of fish > 100 mm in November. Thus, there must also have been anomalous movement in or out of steep angle habitats such that larger fish were under-represented in September and/or over-represented in November.

Table 5.1. Most likely parameter estimates of 5 models fit to the 2004 length frequency data from Glen Canyon. See text for description of models and parameters definitions. Survival rates are for the period beginning on the specified date until one day before the date in the following row.

		Constant Survival					
Model Name		ConstSurv-BetaRec		ConstSurv-WeekRec			
Recruitment Model		Beta Distribution		Independent Weekly			
# Parameters		10		56			
-'ve Log-Likelihood		1455		1016			
Hatch Mode		Apr-15		Apr-22 & May-20			
Habitat Type		Low	Steep	Low	Steep		
VulHalf		28.84	40.91	28.90	40.57		
VulSI		100.00	9.30	100.00	9.61		
MovHalf		423.88		431.74			
MovSI		1.00		1.00			
Survival Rate		0.86	0.84	0.86	0.84		
		Variable Survival					
Model Name		VarSurv-BetaRec		VarSurv-WeekRec		VarSurv-ConstSurvBetaRec	
# Parameters		22		68		20	
-'ve Log-Likelihood		1000		843		1199	
Hatch Mode		Feb-20		Apr-22 & May-20		= ConstSurv-BetaRec	
Habitat Type		Low	Steep	Low	Steep	Low	Steep
VulHalf		28.80	40.20	29.04	40.50	28.59	39.19
VulSI		100.00	9.36	100.00	8.80	100.00	8.91
MovHalf		550.31		402.66		424.39	
MovSI		1.18		1.01		1.00	
Survival Rate	1-Apr	0.77	0.87	0.83	0.95	0.85	0.95
	6-May	0.93	1.00	0.86	1.00	0.93	0.92
	10-Jun	0.76	1.00	0.79	1.00	0.82	1.00
	1-Jul	0.89	0.91	0.87	0.92	0.91	0.95
	5-Aug	0.78	0.85	0.90	0.86	0.84	0.85
	9-Sep	0.79	0.90	0.85	0.92	0.87	0.90
	4-Nov	0.85	0.60	0.76	0.59	0.96	0.59

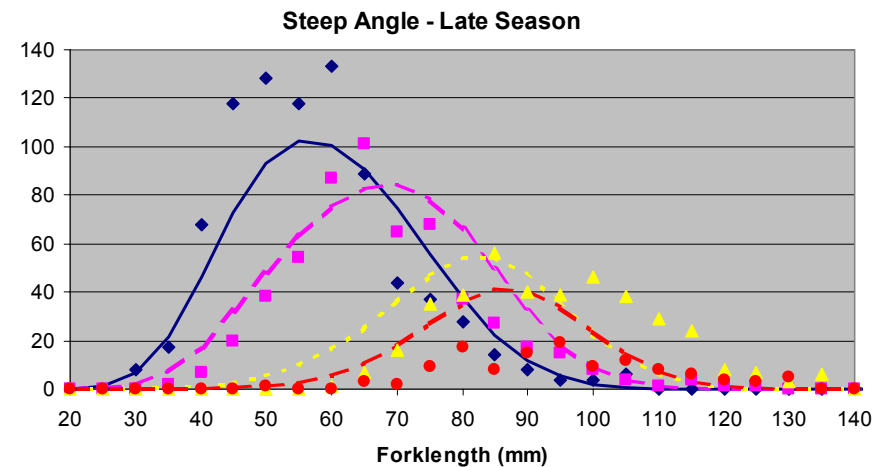
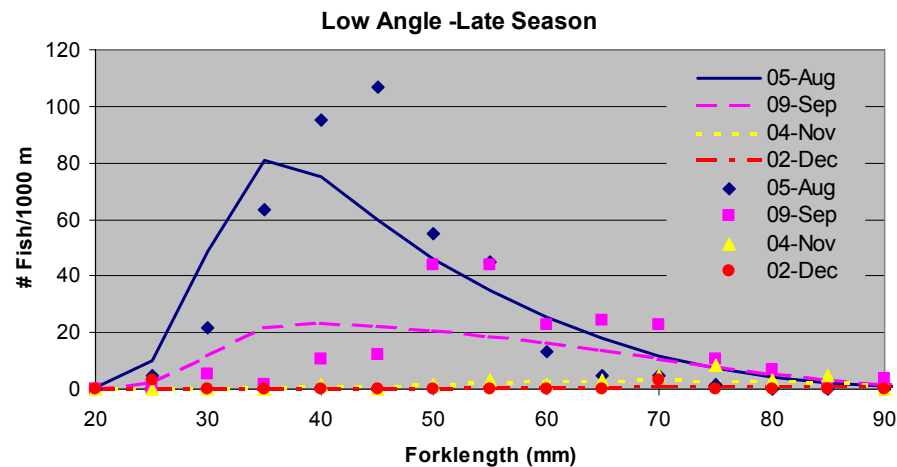
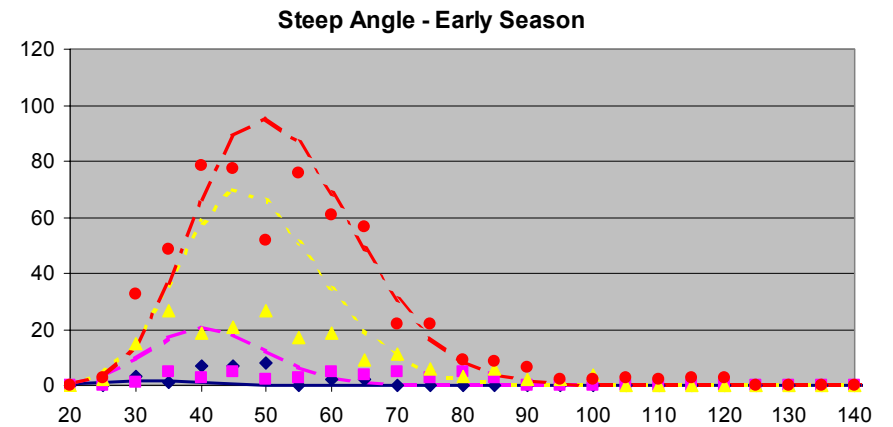
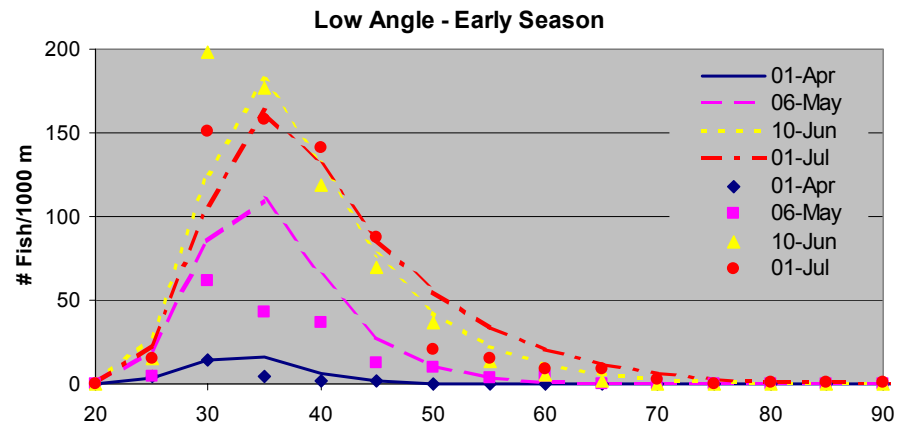


Figure 5.1. Observed (points) and predicted (lines) length frequencies in Glen Canyon in 2004, assuming that survival rates are constant across sample periods and where hatch timing is predicted by estimating parameters of a beta distribution (ConstSurv-BetaRec).

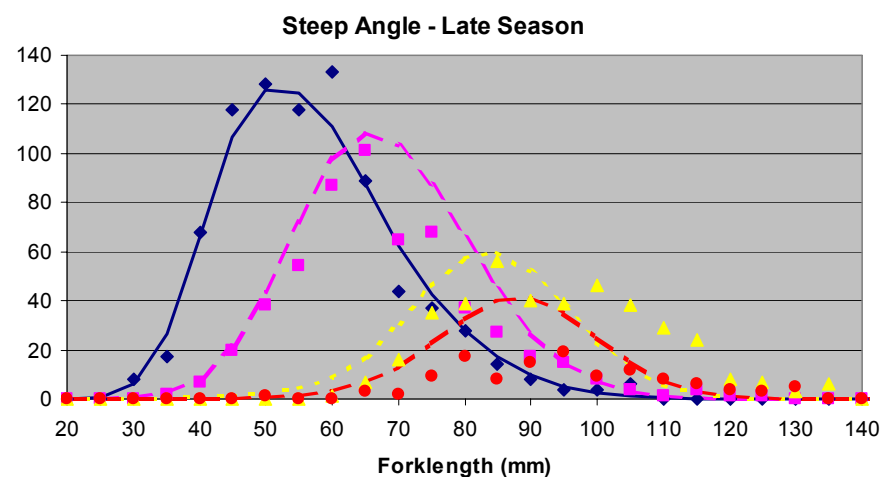
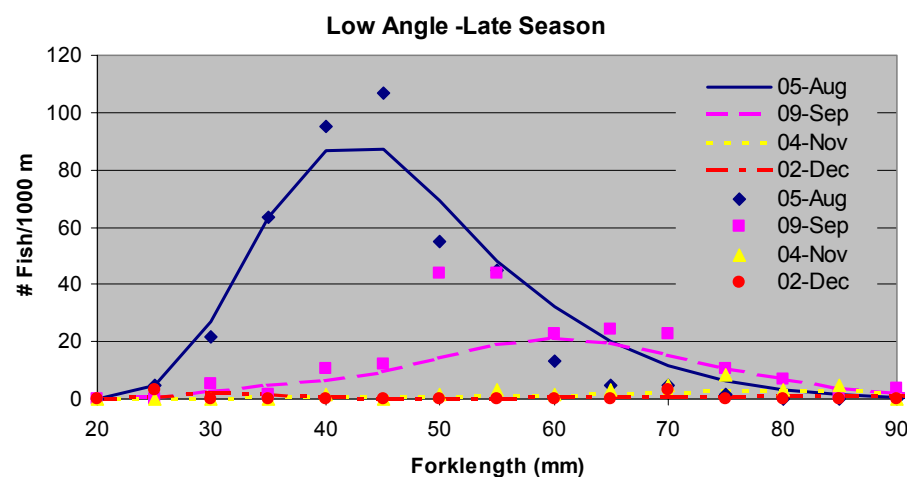
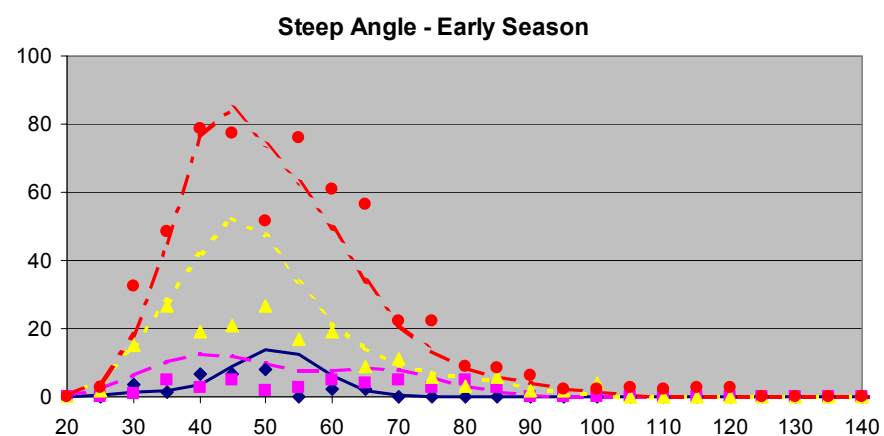
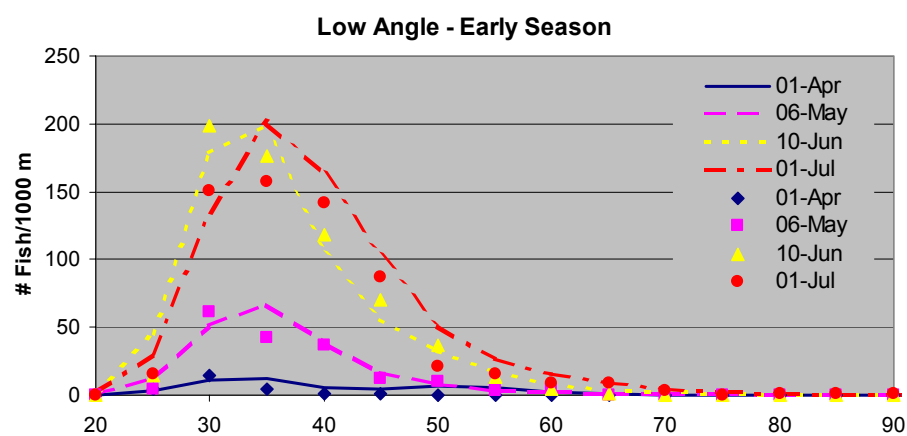


Figure 5.2. Observed (points) and predicted (lines) length frequencies in Glen Canyon in 2004, assuming that survival rates are constant across sample periods and where hatch timing is predicted by independent weekly estimates (ConstSurv-WeekRec).

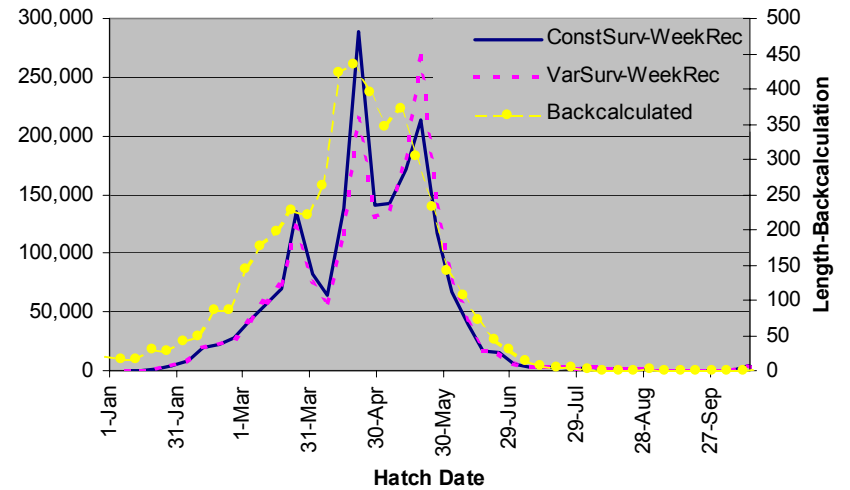
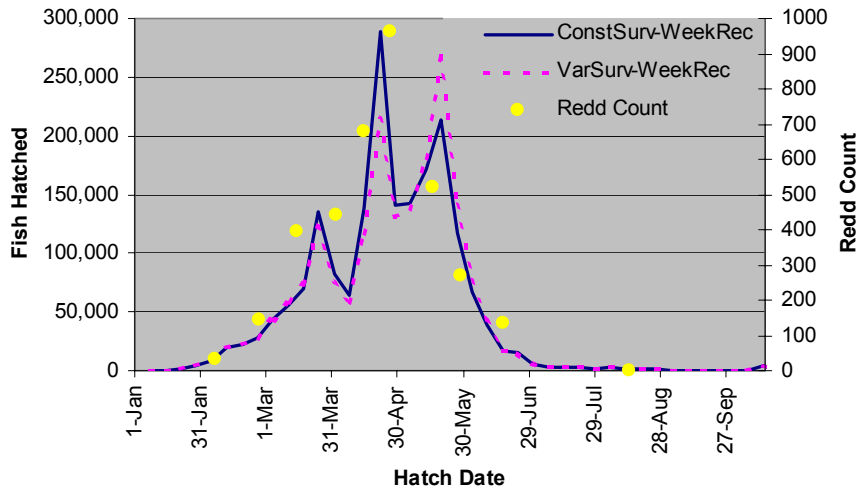
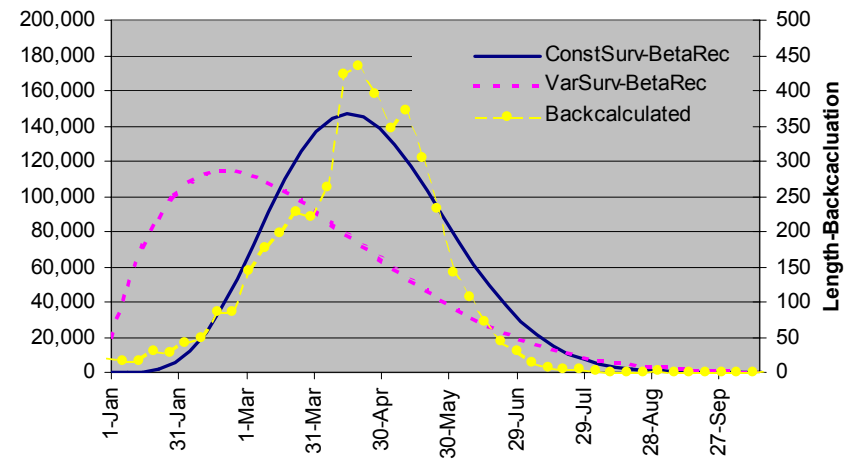
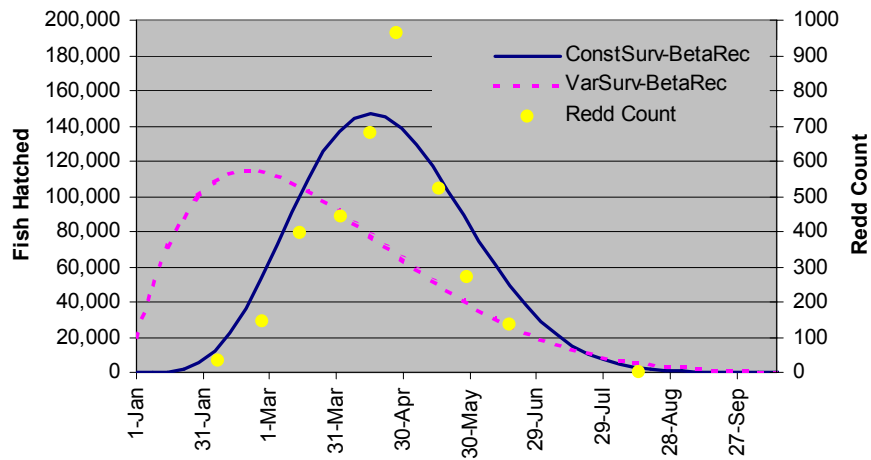


Figure 5.3. Predicted hatch date distributions based on constant (ConstSurv) and variable (VarSurv) survival rates across sample periods and where hatch timing is predicted from a beta distribution (BetaRec) and from independent weekly estimates (WeekRec). Redd counts, advanced to the estimated hatch date based on intergravel water temperatures, and the hatch date distribution based on a length back-calculation are also shown.

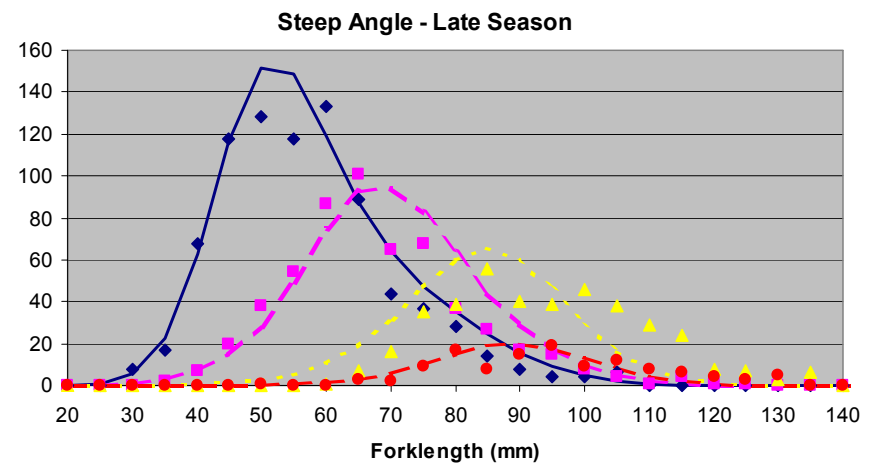
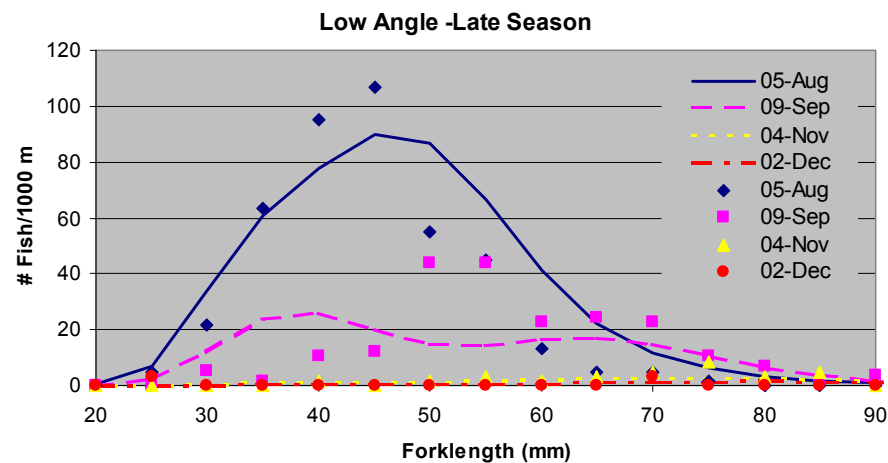
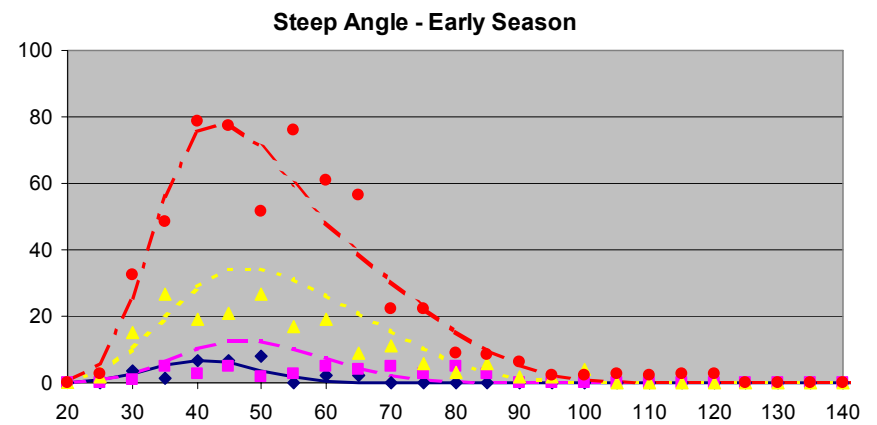
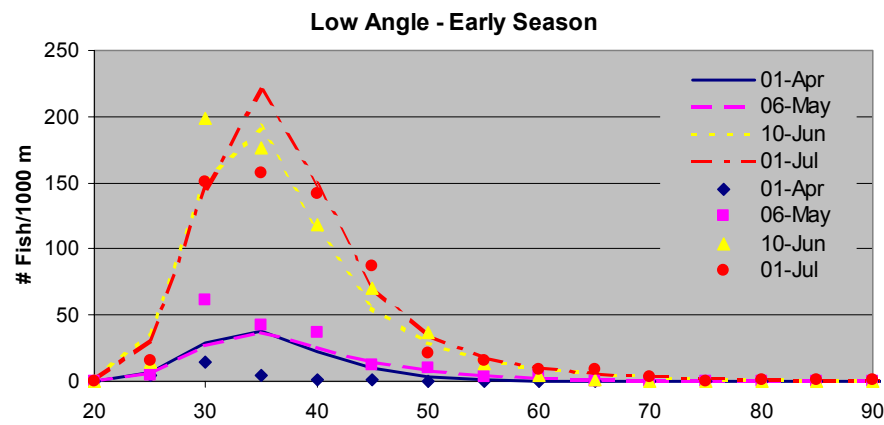


Figure 5.4. Observed (points) and predicted (lines) length frequencies in Glen Canyon in 2004, assuming variable survival rates across sample periods and where hatch timing is predicted by estimating parameters of a beta distribution (VarSurv-BetaRec).

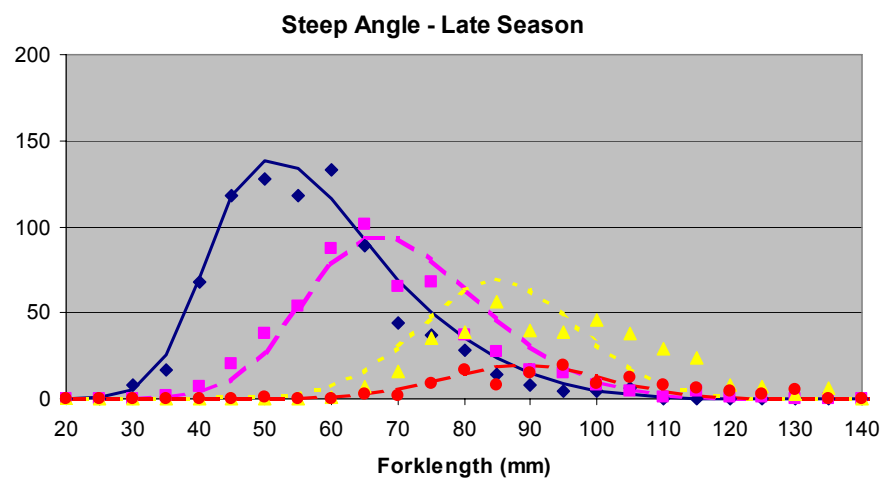
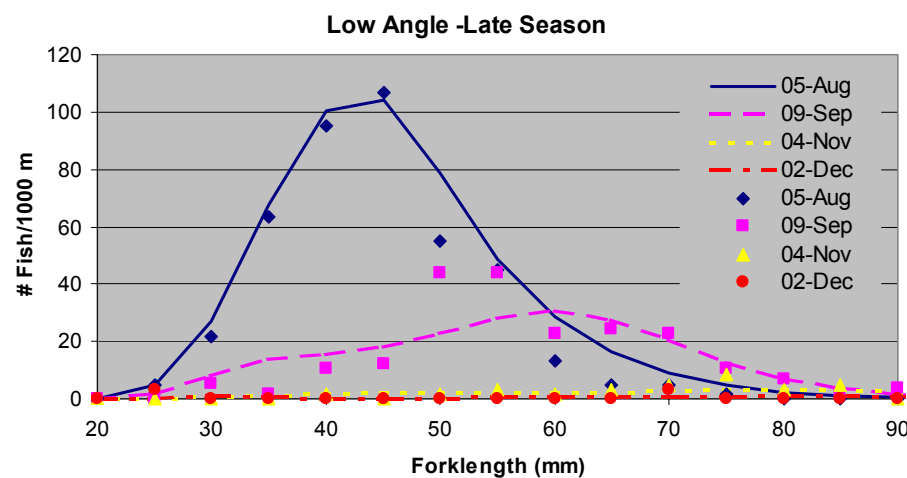
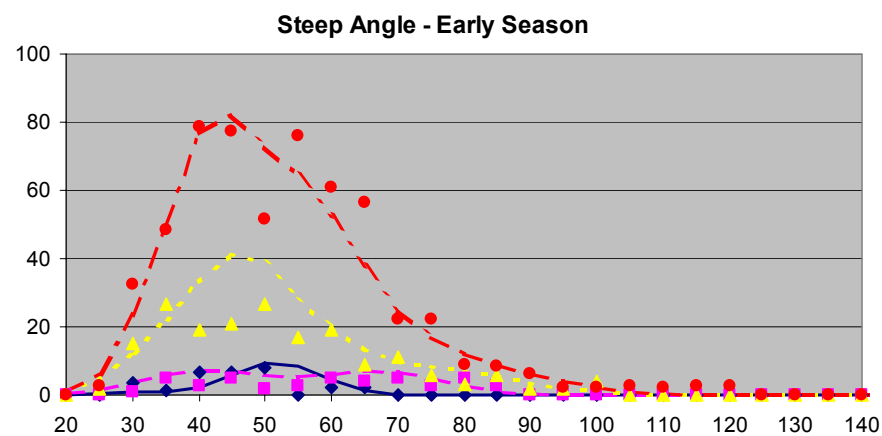
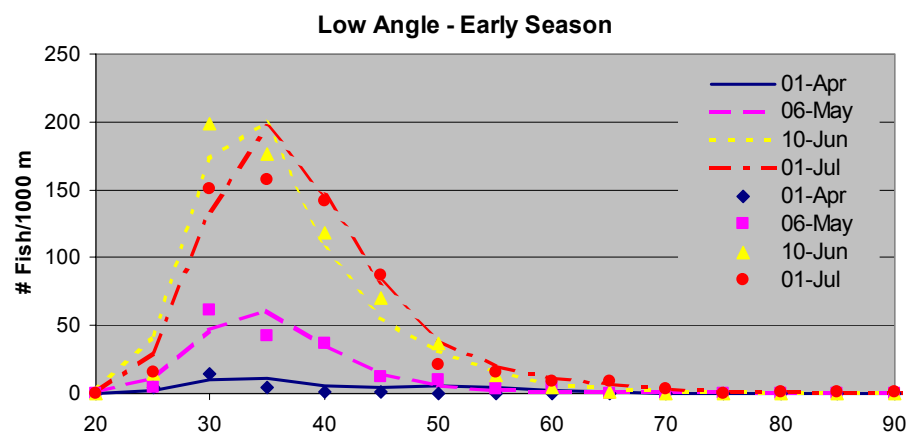


Figure 5.5. Observed (points) and predicted (lines) length frequencies in Glen Canyon in 2004, assuming variable survival rates across sample periods and where hatch timing is predicted by independent weekly estimates (VarSurv-WeekRec).

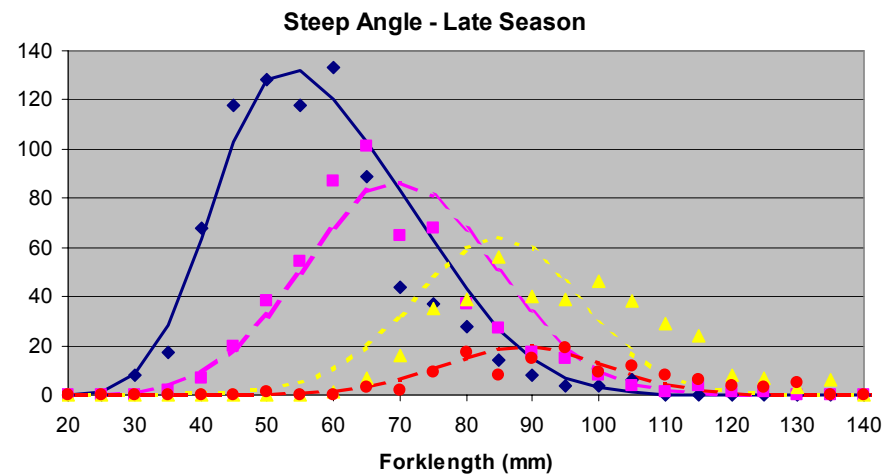
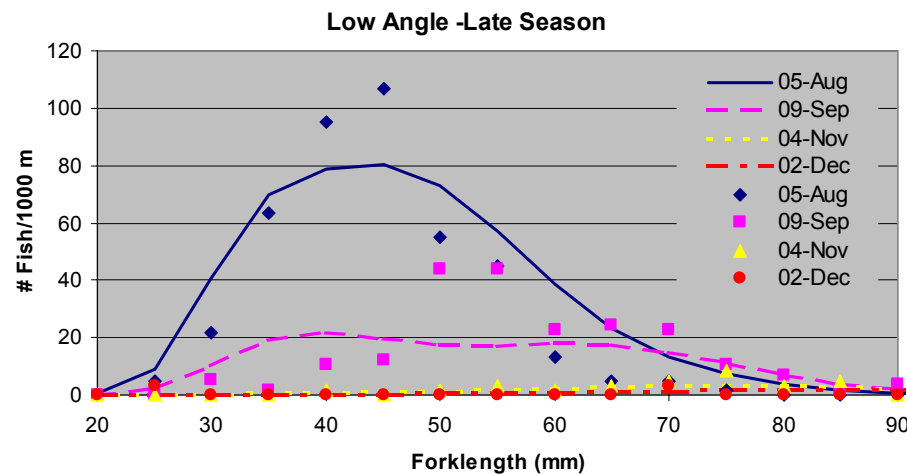
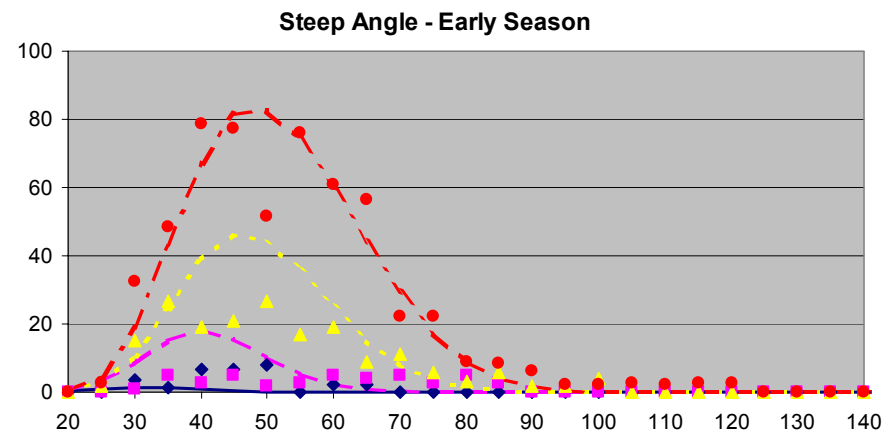
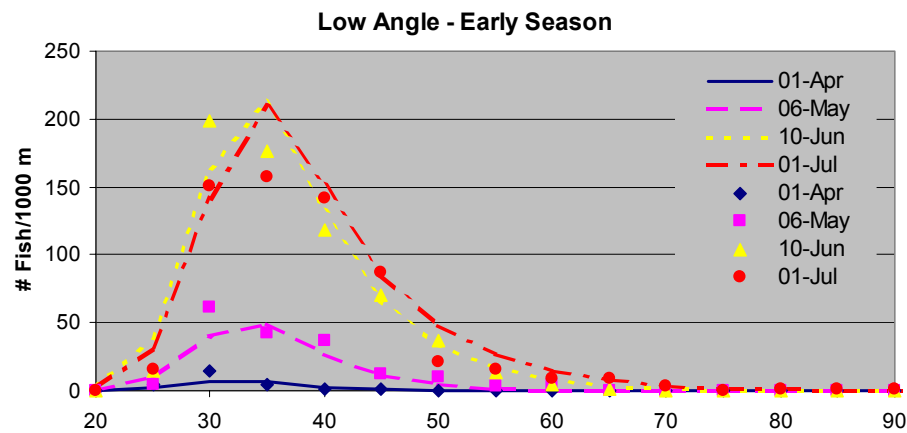


Figure 5.6. Observed (points) and predicted (lines) length frequencies in Glen Canyon in 2004 assuming variable survival rates across sample periods and where hatch timing is predicted based on the most likely parameters for the beta distribution used to estimate recruitment for the constant survival rate model (VarSurv-ConstSurvBetaRec).

The constant survival rate model, regardless of the recruitment-timing distribution, substantially over-predicted the number of 70-100 mm fish for the December 2004 sample period in steep habitats. The most obvious explanation here is that there was a reduction in the survival rate between the November and December sampling sessions, possibly related to the 42.5 kcfs high-flow test that occurred in late-November. There was no lateral shift in the observed length frequency between November and December. This suggests that there was either no growth between this period as our logistic model basically predicts (Fig. 4.9), that there was increased mortality of larger fish between November and December, or perhaps most likely, that there was increased movement of larger fish out of the type of steep angle habitats that we sampled.

The variable survival models (VarSurv-BetaRec and VarSurv-WeekRec) produced statistically significant better fits to the data (Type I error < 0.0001) relative to the equivalent constant survival models (Table 5.1, Fig.'s 5.4 and 5.5). The variable survival model with hatch timing predicted by the beta distribution had fewer parameters ($n = 22$) than the constant survival model with independent weekly recruitment ($n = 56$) but provided a better fit to the length frequency data. However, the most likely recruitment timing from the variable survival model predicted that over 50% of the hatch had occurred by early-February (Fig. 5.3). This prediction is undoubtedly wrong as there was very little spawning prior to January (Fig. 2.4a) and no evidence of a large hatch in January or February based on the length back-calculated hatch dates (Fig. 4.13). The independent weekly recruitment estimates from the variable survival model are close to those from the constant survival model and in good agreement with the hatch date distributions based on redd counts and length back-calculations. Although not shown here, we noted substantial uncertainty in hatch timing under the variable survival model. A plausible fit to the length frequency data was also obtained by using the most likely beta distribution-recruitment timing parameters from the constant survival model, but allowing survival rates to vary between sample periods (Fig. 5.6).

A comparison of discrepancies between observed and predicted length frequencies based on constant and variable survival rate models was sometimes helpful to

untangle the effects of movement, recruitment, and survival seen in the data. The over-prediction of 30-40 mm fish in May based on constant survival (Fig. 5.1), which was reduced when more flexibility in hatch timing was allowed (Fig. 5.2), was also reduced by allowing survival rate to decline between April and May under the more restrictive hatch timing model (Table 5.1). Hatch timing and survival rates are confounded in samples taken early in the season and we cannot ascertain whether the lower than expected abundance in May in low angle habitats was caused by lower than expected survival in April or due to non-smooth trends in hatch timing that are not well described by the beta distribution. The variable survival model with or without independent weekly recruitment estimates (Fig. 5.4 and 5.5) could not eliminate the over-prediction of 40-55 mm fish in June in steep angle habitats. This strengthens our hypothesis that a threshold density or temporal lag is required to initiate significant movement between habitat types. Variation in survival rate between sample periods could also not eliminate the under prediction of fish larger than 100 mm, and over prediction of smaller fish, in November 2004 in steep habitats. This strengthens our hypothesis that this discrepancy was caused by higher growth rates late in the season owing to increased water temperatures not captured by our length-at-age model, coupled with under-or over-representation of larger fish in the September or November samples, respectively.

The variable survival model did a much better job at predicting the very low densities observed in December in steep habitats relative to the constant survival model. In steep habitats, weekly survival rates dropped from 0.90 for the period spanning early-September to early-November, to 0.59 for the period between early-November and December (Table 5.1). A substantial drop in the number of fish between August and September in low angle habitats, and a moderate drop in steeper habitats were also observed. Survival rates for the period between the August and September samples for low and steep angle habitats of 0.84-0.85, predicted by the variable survival model using a realistic hatch timing pattern (VarSurv-ConstSurvBetaRec), were noticeably lower than in the previous (0.91 and 0.95) and following intervals (0.87 and 0.90). The decrease in the August-September survival rate in steep habitats occurred under all hatch timing

models as it did in low angle habitats, with the exception of the weekly recruitment model (VarSurv-WeekRec).

5.2.2 Model Dynamics and Uncertainty

A likelihood profile of the survival rate in low angle habitat from the simplest model (ConstSurv-BetaRec) was used to clarify the interactions between catchability, movement, and the survival rate in steep habitats. Very low survival rates, that resulted in catchabilities above the constraints of 0.05 and 0.10 for low and steep angle habitats were very unlikely, resulting in the steep left-hand edge of the probability distribution (Fig. 5.7). As the survival rate increased to a point where the catchability constraint in low angle habitats was no longer binding, probabilities rose quickly. The most likely survival rate was reached at a point where it gave the best fit to the data in low angle habitats while at the same time providing just enough immigration to steep habitats to escape the catchability constraint. The survival rate in steep habitats, which was allowed to vary, was then optimized by the search procedure to provide the best fit to the data in this habitat type. The slope of the descending limb of the survival rates profile is determined by increasingly weaker fits to the data from both low and angle habitats. The additional fish immigrating to steeper habitats were for the most part absorbed by the catchability computation in steep habitats.

There was more uncertainty in the survival rate from low angle habitats compared to that in steeper habitats (Fig. 5.8) because the sample size in steep habitats (3,000 fish) was double that from low angle ones (1,500 fish). Catchability constraints in part determined the most likely survival rate estimate and also influenced the extent of uncertainty. Setting the constraint on catchability to one, resulted in a large decrease in the MLE survival rate in low angle habitat. That is, survival rate could be much lower when we admitted that the complete population of hatched fish from the reach that we specified (2,000,000) could be caught in our limited sampled area. The probability of higher survival rates in steep habitats was only slightly larger under the $q_L=1/q_S=1$ scenario compared to the $q_L=0.05/q_S=0.10$ scenario. Larger probabilities of higher

survival rates were required to compensate for the larger probabilities of lower survival rates in low angle habitats. There was no detectable difference in the likelihood profiles under the $q_L=0.05/q_S=0.10$ when recruitment timing parameters were allowed to vary.

Uncertainty in monthly survival rates (VarSurv-ConstSurvBetaRec) varied seasonally and differed among habitat types (Fig. 5.9). Survival rates in low angle habitats in September and November were more uncertain than previous months because of low sample size. The additional large uncertainty in the November 2004 estimate occurred because survival rates in one month influence predictions in subsequent ones. Uncertainty in the survival rate for the period between the second-to-last and last sample will therefore always be highest as there will be no subsequent observations to better define it. The lack of overlap in probability profiles in low angle habitats for June and July implies that there was a large difference in survival rates. However, examination of the observed and predicted length frequencies shows that the June survival rate was likely under-predicted as a means of compensating for non-linearity's or lags between fish density and movement rates not accounted for in our model structure (Fig. 5.6). The survival rate after the August sample in low angle habitats was significantly lower than the survival rate in July, and there was a reasonable probability that it was also lower than the rate in September.

Survival rates were much better defined in steep angle habitats than in low angle ones (Fig. 5.9). The total sample size in steeper habitats was double that in lower angle thus the penalty for unlikely survival rates in the steeper habitat type was more severe. The survival rate after the August sample period was significantly lower than that in the previous and following months. The November survival rate was most uncertain because, as for the low angle habitat, there was no subsequent sampling to better define it. In spite of this uncertainty, there was no overlap with probability profiles for other months, implying that the survival rate between the November and December sampling periods was significantly lower.

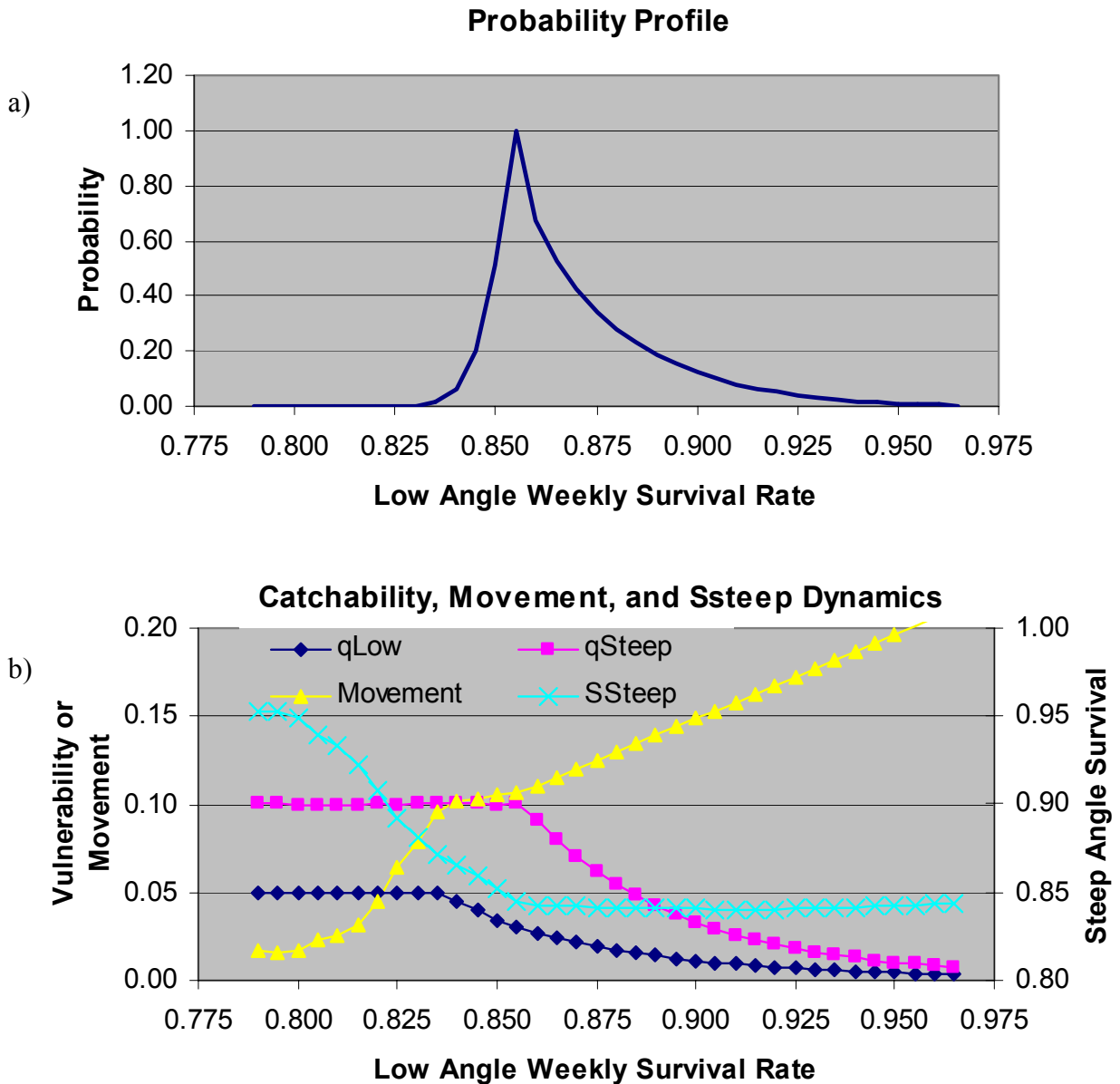


Figure 5.7. Probability profile of the survival rate in low angle habitat (a), and most likely estimates of movement from low to steep angle habitat (proportion of fish 50 mm in length), survival rate in steep habitat (Ssteep), and catchabilities in low (qLow) and steep (qSteep) habitats as a function of the profiled low angle survival rate (b). Profiles were based on the constant survival rate model using the most-likely estimate of weekly hatch timing based on the beta distribution (ConstSurv-BetaRec).

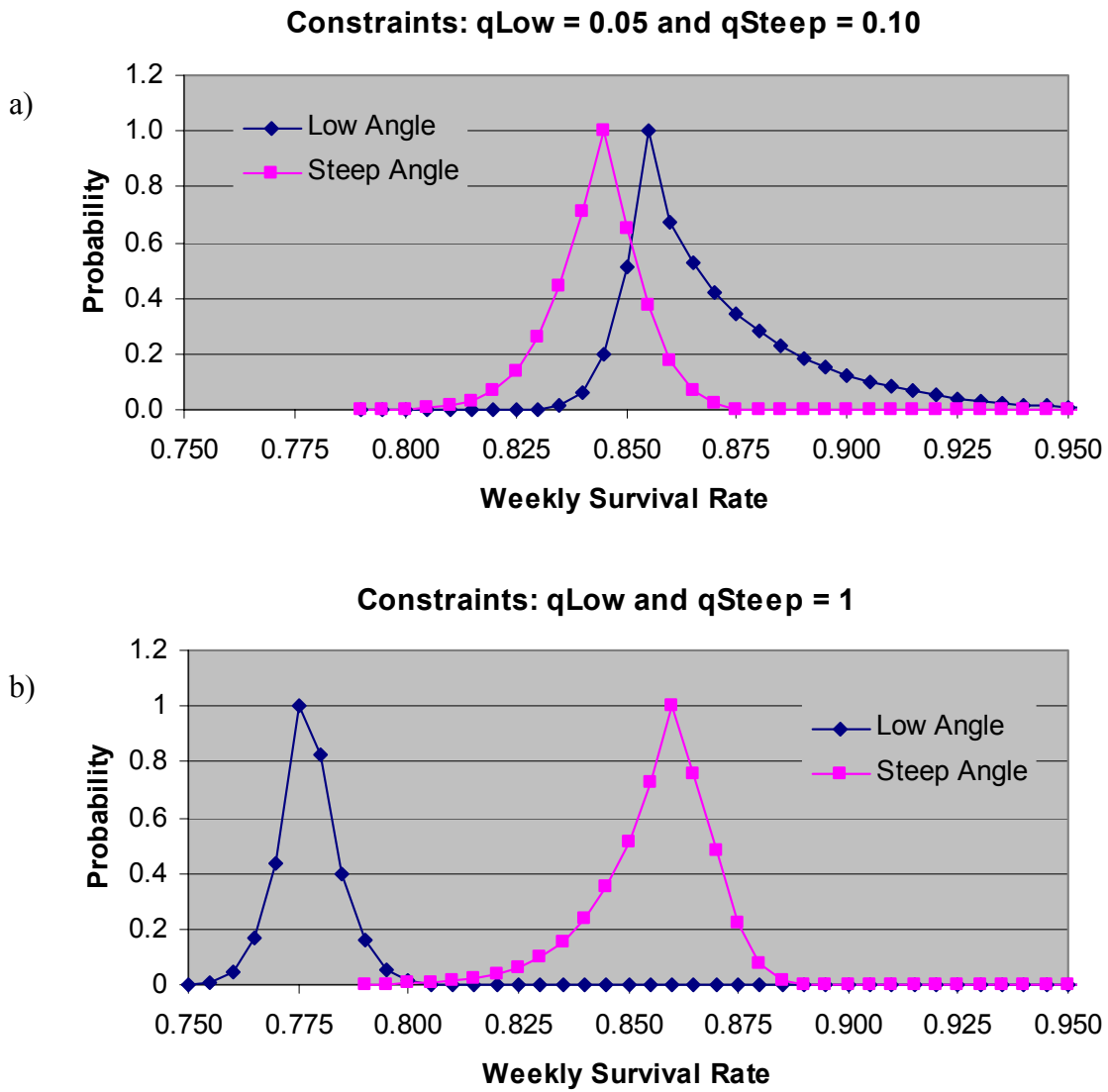


Figure 5.8. Probability profiles of the weekly survival rate in low and steep angle habitats assuming catchability constraints in low (qLow) and steep habitats (qSteep) of 0.05 and 0.01, respectively (a), and 1 (b). Profiles were based on the constant survival rate model using the most-likely estimate of weekly hatch timing based on the beta distribution (ConstSurv-BetaRec).

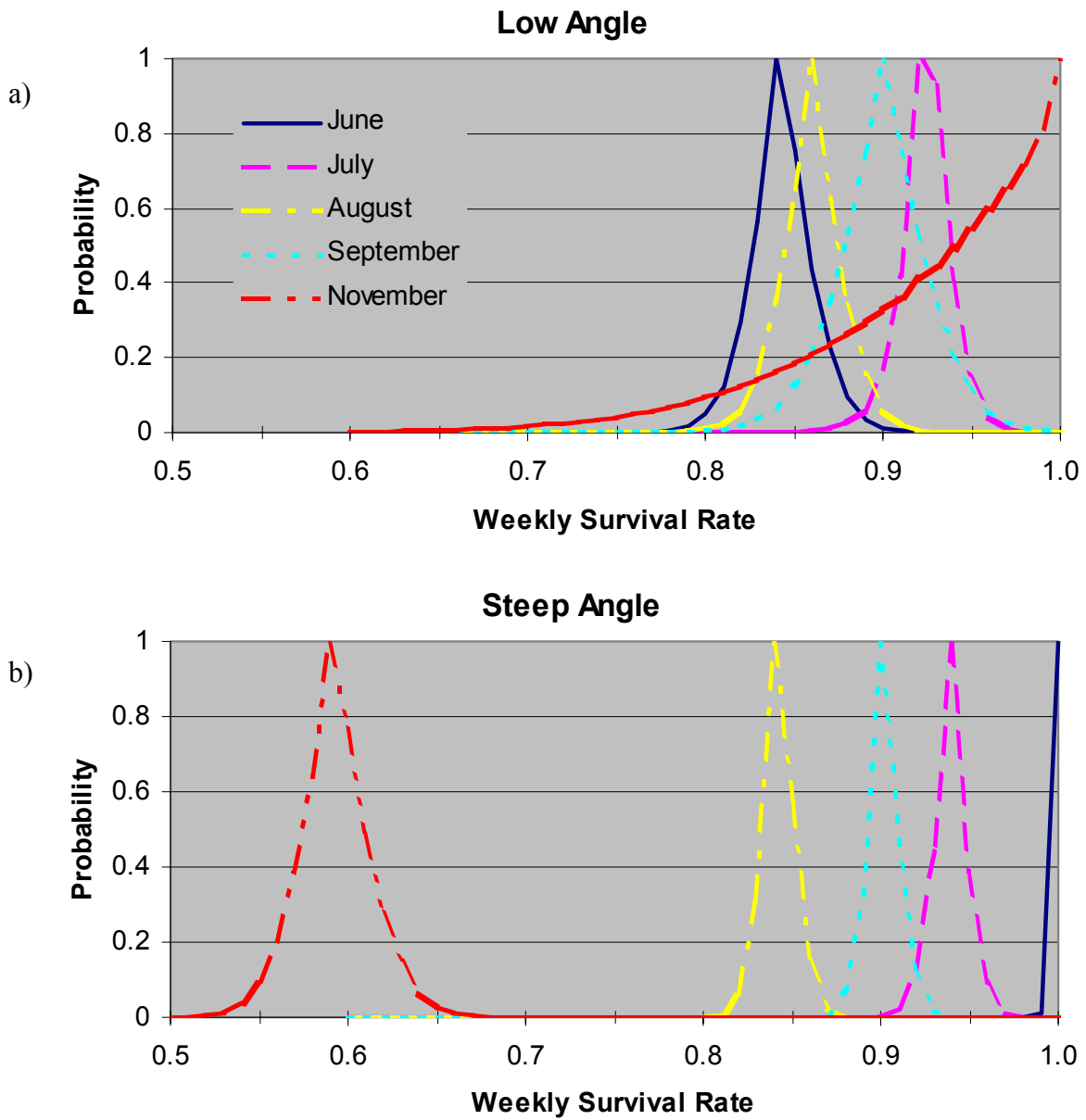


Figure 5.9. Probability profiles of the weekly survival rate in a) low and b) steep angle habitats. Profiles were generated allowing variation in survival rates among sample periods and using the best-fit beta distribution parameters for the weekly hatch timing pattern from the constant survival rate model (VarSurv-ConstSurvBetaRec).

5.3 Conclusions from Stock Synthesis Modelling

Constant survival rate estimates were dependent on the rate of movement, and differences in catchability and survival rates among habitat types. For example, estimates of reduced survival rates in low angle habitats were only likely if movement rates were low and if catchability and survival in steep habitats was high (Fig. 5.7). In spite of this potential confounding, the probability profiles of survival rates were relatively narrow because of the assumed model structure and the high-resolution dataset. It should be stressed that the survival rate estimates provided here are conditional on catchability constraints (Fig. 5.8). Survival rates in low angle habitat would be much lower, and slightly higher in steep angle habitat, if we allow for the unlikely possibility that catchabilities could be higher than our constraints of 0.05 and 0.10. From a long-term monitoring perspective, where the key policy comparison is the inter-annual difference in survival rates, the dependence of survival rate on catchability will not matter if it is assumed that catchability does not vary among years. This assumption might be problematic in fisheries stock assessments where the data are collected by fisherman who constantly optimize the quality of their effort or change the distribution of the stock, but is probably reasonable for scientific surveys conducted in relative stable physical environments such as the reach immediately below Glen Canyon Dam. An inter-annual comparison of survival rates would be accomplished through the joint estimation of catchability and size-vulnerability parameters across years while allowing hatch timing, magnitude, and survival rates to vary.

The constant survival rate models predicted a hatch timing that was very similar to an independent estimate based on redd counts (Fig. 5.3). Predictions were also very similar to the length back-calculated hatch date distribution. In our case, where sampling occurred prior to, during, and after, the entire hatch became vulnerable to the gear, the resulting back-calculated hatch date distribution was very stable (Campana and Jones 1992). In situations with a less thorough sampling regime the model provides a reasonable way to account for the effects of vulnerability and cumulative mortality that lead to instability in back-calculated distributions. We saw evidence that hatch timing-

patterns can be biased, or at least highly uncertain, when we admitted that survival rates vary across sample periods (Fig. 5.3). That is, if one is interested in discerning temporal variation in hatch timing, then it is necessary to assume constant survival rates or to at least to reduce the number of periods when survival is allowed to vary. In our case, where we had an independent means of evaluating the predicted hatch date distribution, we could hold hatch timing fixed when allowing survival rates to vary over time in the more complex survival model (e.g. VarSurv-ConstSurvBetaRec). This in turn reduced the extent of parameter confounding and increased the inferences and certainty of the assessment of temporal changes in survival. More work is required to explore how the extent of confounding between survival rate and hatch timing is influenced by sample size and frequency, variation in length-at-age, and the desired temporal resolution of the predictions.

We did not attempt to estimate the magnitude of the annual hatch because we computed catchability at its maximum likelihood estimate conditional on other model parameters. Based on a single year of data, higher estimates of hatch magnitude would be completely compensated by lower estimates of catchability, and visa-versa. However, it would be possible to estimate the magnitude of hatch when multiple years of data are included in the analysis and catchability is assumed to be constant across years. Estimates of the relative difference in hatch magnitude among years, combined with an independent index of egg deposition through redd or spawner surveys, allows the computation of an annual egg-to-emergence survival index.

The variable survival model was a powerful tool for interpreting seasonal differences in length frequency data and for relating seasonal differences in survival rates to dam operations. The failure to fit the June length frequency in steep habitats could not be corrected by allowing survival (Fig. 5.4) or hatch timing (Fig. 5.5) to vary, providing a relatively strong indication of threshold or lag effects in the density-movement relationship. From a simple comparison of the length frequency data, there was no way to separate movement and catchability differences between habitat types from changes in survival during the August to September period (e.g. Fig. 5.1). The model predicted

reduced survival over this period relative to other months (Fig. 5.9), which may have been caused by the reduction in the daily minimum flow from 10 to 5 kcfs in early-September. However, it is also possible that the decrease in survival we estimated was a natural occurrence, possibly driven by a normal ontogenetic habitat shift and/or density-dependent mortality. The modeling and monitoring framework presented here is not a complete substitute for an informative experimental design. To rule out this alternate hypothesis, the minimum flow change would have to be conducted earlier in the season or eliminated, and the experiment would need to be replicated over multiple years.

Sampling limitations or deficiencies, and assumptions determined by the model structure, can lead to weak or incorrect inferences. We estimated a very large decrease in survival rate between the November and December samples, which could have been caused by the 42.5 kcfs high-flow test. However we feel the inference here is quite weak because it is very possible that by December, fish were reaching a size where they would move out of our sampling universe into habitats with deeper and faster water. Sampling obviously needs to cover the full range of habitats used over the period for which an inference is needed, which did not occur in this example. This same class of problem was seen with the possible failure of our growth model to fit the November length frequency data. By November a good portion of the 2004 cohort had grown beyond the size range from which we could afford to take sufficient age samples. As a result, we were uncertain whether we underestimated length-at-age by late-fall and early-winter, or whether there was an over-representation of larger fish in the November sample owing to a natural or dam-induced process.

The juvenile stock synthesis modeling approach we have developed represents a potential advance in monitoring the response of salmonid populations to habitat alterations. Measuring trends in only the abundance of adult populations is informative only if management treatments are implemented consistently and with adequate replication. Based on the current track record of most adaptive management programs, there are unfortunately few examples where this is the case (Walters 1997). More often than not, the politics of multi-stakeholder settings and natural variation in hydrology result in a very haphazard implementation of treatments that are generally impossible to

untangle through subsequent examination of adult abundance time series. The intensive juvenile monitoring program presented here, that measures responses on shorter time-scales that are more consistent with the duration of management treatments, may be required element for adequate learning in these settings. However, we caution that a juvenile monitoring program does not replace the need to track trends in the adult population. Without this crucial data it will be uncertain whether increased mortality at an early juvenile stage is compensated by a subsequent reduction in density-dependent mortality.

6.0 Natural Reproduction of Rainbow Trout in Marble Canyon

Rainbow trout in Grand Canyon potentially compete with and consume native fish. The extent and nature of natural reproduction of rainbow trout below Lees Ferry determines the extent to which changes in the operation of Glen Canyon Dam can reduce it. Obviously, if there is limited mainstem spawning and rearing of young fish below Lees Ferry, altering flows to reduce the survival rate of early life stages in this reach will not be very effective. If the population of trout in Marble Canyon is supported by downstream dispersal from Glen Canyon, then changes in the production of young fish in Glen Canyon will have effects on the population downstream.

A number of studies have provided information relevant to the question of whether the population of rainbow trout in Grand Canyon is sustained by downstream dispersal of individuals from Glen Canyon or by natural reproduction from tributaries or the mainstem below Lees Ferry (Fig. 1.1). Approximately 400,000 dye-marked stocked fingerling trout, typically between 75 and 115 mm, were released at Lees Ferry between 1983 and 1986 (Maddux et al. 1987). During this period, 61% of the catch in Glen Canyon was comprised of dye-marked fish compared to only 7% of the catch in Marble Canyon. These data indicate that some fish migrated downstream, but the magnitude of the dispersal rate is confounded by potentially different rates of natural reproduction and survival between the two reaches. The Arizona Game and Fish Department stocked 78,000 and 73,000 rainbow trout with coded wire nose tags in 1992 and 1993, respectively (Valdez and Ryel 1995). Of nearly 8,000 rainbow trout captured downstream of Lees Ferry, only 3 of these fish were recaptured, and all were within 3.5 miles of Lees Ferry. A total of 9,642 adult rainbow trout were tagged throughout Glen and Grand Canyon between 1984 and 1986, and 641 of those fish were recaptured (Maddux et al. 1987). The proportion of fish moving in a downstream direction was more than double that of fish moving in an upstream direction or that remained relatively stationary. Unfortunately, the proportion of fish tagged in Glen Canyon that were later recaptured in Marble Canyon was not reported. Considerable spawning in Nankoweep, Bright Angel, and Deer Creeks was documented in the 1980s and early 1990s (Maddux et al. 1987,

Valdez and Ryel 1995). Together, these observations have somehow led to the common belief that the rainbow trout population in Marble Canyon is solely sustained by natural reproduction in tributaries or the mainstem below Lees Ferry, and that downstream dispersal from the population in Glen Canyon is negligible. If this hypothesis were still applicable to the current population in Marble Canyon, removing adults from the mainstem through mechanical removal in the vicinity of the Little Colorado River (LCR) would only need to be conducted for a few years until the local population was depleted. On the other hand, if rainbow trout in Glen Canyon are dispersing downstream in significant numbers, mechanical removal of rainbow will need to be repeated on a continuing basis. In addition, if downstream dispersal from Glen Canyon is density-dependent as has been shown for other salmonid populations (Lister and Walker 1966, Ruggles 1966), then flow management decisions that influence the density of rainbow trout in Glen Canyon will also affect densities in Grand Canyon.

The conventional wisdom that rainbow trout in Marble Canyon originate from local reproduction needs to be reexamined in light of two significant changes to the Colorado River ecosystem in the last decade. Conclusions on the extent of downstream dispersal of rainbow trout drawn from studies conducted in the 1980s and early 1990s, when densities in Glen Canyon were much lower (McKinney et al. 1999), may no longer be applicable (Figure 6.1). Increases in rainbow trout densities in Marble Canyon could have resulted from higher rates of downstream dispersal from Glen Canyon owing to improved reproductive success in Glen Canyon associated with ROD flows. The multi-year lag between increased densities in Glen Canyon and those downstream support this possibility (Fig. 6.1 top). The alternate hypothesis, that rainbow trout spawning habitat in the mainstem below Lees Ferry has increased since the late 1990s owing to reduced fine sediment inputs from the Paria River, also provides a feasible explanation for higher trout densities in Marble Canyon. This hypothesis seems less likely as the increase in densities below Lees Ferry began in the mid 1990s, 5 years prior to the period of reduced sediment input from the Paria (Fig. 6.1). Another possible explanation is that most spawning occurs in tributary streams (Nankoweap, Bright Angel Creek, Clear Creek) and stabilized

flows under the ROD have increased the survival rate of young trout once they enter the mainstem.

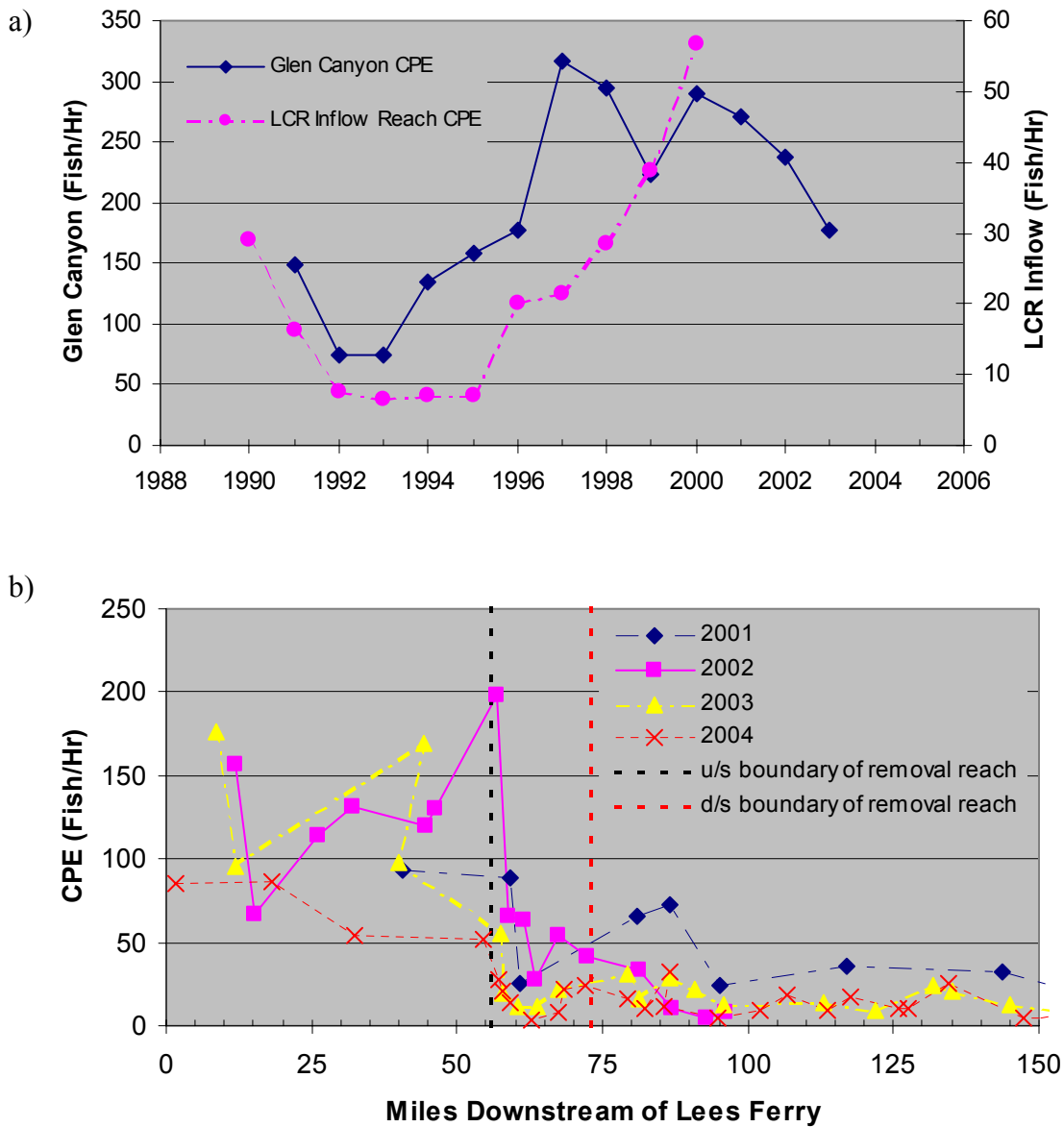


Figure 6.1. Inter-annual trends in catch-per-effort (CPE) from boat electrofishing in Glen Canyon and the LCR inflow reach (a) and the spatial trend in CPE from Lees Ferry to river mile 150 from 2001 through 2004 (b). Data provided by Arizona Game and Fish Department.

In this study, we evaluated the extent and nature of reproduction in Marble Canyon through a comparison of spawning habitat, redds densities, and YoY abundance in Glen and Marble Canyons. Documentation of significant amounts of rainbow trout spawning habitat in the mainstem or tributaries of Marble Canyon would support the notion that rainbow trout in this reach could potentially be self-sustaining. Redd surveys that provide direct evidence of significant spawning activity in the mainstem below Lees Ferry or in Nankoweep Creek would provide much stronger inferences than those drawn from spawning habitat surveys. A comparison of spatial and temporal patterns in YoY abundance, growth, and hatch timing in Glen and Marble Canyon provides a means for estimating the relative magnitude of local reproduction in some cases. For example, the absence of YoY in Marble Canyon would suggest that there was no, or very limited, local reproduction, at least in the year of the survey. Alternatively, the presence of YoY in Marble Canyon during the winter and spring prior to the emergence of YoY in Glen Canyon would provide convincing evidence of local reproduction. Differences or similarities in growth and hatch timing between Glen and Marble Canyons could help strengthen inferences about the origin of YoY fish captured in Marble Canyon.

6.1 Methods for Spawning, Redd, and YoY Surveys in Marble Canyon

Surveys of the Colorado River between Lees Ferry and the confluence of the Little Colorado River were conducted on April 3-9, June 11-16, and August 9-12, 2004. Spawning habitat, redd, and YoY surveys were conducted on the April and June trips while only a YoY survey was conducted on the August trip. The YoY survey on the June trip was extended from the LCR confluence to river mile 75. A description of methods for the spawning habitat and redd surveys is provided in Section 6.1.1. Methods for the YoY survey are provided in Section 6.1.2.

6.1.1 Spawning Habitat and Redd Surveys

Spawning habitat and redd surveys were conducted during daylight hours at close to the minimum daily flow. The location of suitable spawning habitat or redds was recorded on hardcopies of the GCMRC shoreline habitat map (Mietz 2003). Suitable

spawning habitat was determined based on substrate criteria developed from the spawning habitat study conducted in Glen Canyon in 2003 (Fig. 3.1). Any coarse-grained substrate with a D85 ranging from 10-50 mm was considered suitable. Substrate size was estimated visually by well-calibrated observers who had conducted the spawning habitat assessment in Glen Canyon using quantitative methods. All shoreline areas above the minimum daily flow, which was approximately 8 kcfs during the April trip, and 9 kcfs during the June trip, were surveyed. Submerged areas were surveyed from the deck of a boat or from a clear-bottomed kayak at depths < 3 m and by an underwater video camera for deeper areas (as described in Section 3.1.1). As a complete survey of the entire river bottom between Lees Ferry and the LCR confluence was not possible within the time constraints of our trips, only potentially likely spawning areas were examined. This included pool tail-outs, mid-channel bars, submerged areas near exposed gravel/cobble shorelines on inside river bends, and areas in the immediate vicinity of debris fans and tributary confluences. These features were often associated with morphologies that are known to promote hyporeic flow that has been shown to influence spawning site selection in large rivers (Geist and Dauble 1998). All of the spawning sites that we identified in Glen Canyon were associated with these morphologies. The lower 3 km of Nankoweep Creek was surveyed by foot during the April and June 2004 trips.

6.1.2 Young-of-Year Surveys

The Colorado River between Lees Ferry and the River Mile 75 was divided into five 15-mile sections. Within each section, 20 random sites were selected using the GCMRC shoreline habitat map (Mietz 2003). Ten of these sites were drawn from talus shoreline types and 10 from lower angle shorelines that were classified on the map as cobble bars, sand bars, or debris fans. The same 20 sites were sampled on all three trips. Boat electrofishing was used to sample talus shoreline sites. Unlike Glen Canyon, the majority of low angle sites in Marble Canyon were too deep to sample by backpack electrofishing. On average, 7 of 10 low angle sites were sampled by boat electrofishing, with the 3 shallowest sites sampled by backpack electrofishing. As in Glen Canyon, sampling was conducted at the minimum daily flow which corresponded to the following sampling periods by 15-mile reach: 3:00-10:00 (0-15 mile); 6:00-13:00 (15-30 mile);

9:00-16:00 (30-45 mile); 12:00-17:00 (45-60 mile); and 15:00-22:00 (60-75 mile). Owing to logistical coordination with the mechanical removal trip, we were unable to sample sites below Kwagunt Rapid (river mile 56) on the August trip. YoY sampling methodologies, including the collection of fish for analysis of otoliths microstructure, were identical to those used in Glen Canyon (Section 4.1). Nankoweep Creek was sampled by backpack electrofishing during the April 2004 trip. Two crews, consisting of one person operating the backpack electrofisher and two dippers, surveyed 1.3 km of the lower 3 km of the creek. Site lengths ranged from 60-100 m.

6.2 Marble Canyon Survey Results

6.2.1 Mainstem Spawning Habitat and Redd Surveys

The April 2004 trip coincided with a large flood in the Paria River that limited water clarity in the mainstem Colorado River below the confluence. Turbidity in the mainstem during the April survey never dropped below 100 NTUs and peak values exceed 500 NTUs. At these turbidities, bottom substrate could not be identified at depths as shallow as a few centimeters. We were therefore unable to survey for spawning habitat or redds below the daily minimum flow elevation of 8 kcfs on the April trip. Exposed gravels and cobbles above 8 kcfs were generally much too coarse and poorly sorted for spawning. We observed a handful of very small areas (10-400 m²) that contained appropriate grain sizes for spawning, however no redds were observed at any of these locations (Table 6.1). Note that the April trip occurred shortly after the peak redd count in Glen Canyon which occurred in late-March (Figure 2.4). Assuming a similar spawn timing in Marble and Glen Canyons, our April redd survey was well-timed and it is unlikely that we did not see any redds above 8 kcfs because our survey was conducted either too early or late relative to the spawning season.

Water clarity during the June trip was much better than in April and averaged 2.2 NTUs allowing us to characterize spawning substrate from the deck of a boat and from the clear-bottomed Kayak to a depth of ca. 3 m. We were able to deploy the underwater video camera to survey elevations at depths greater than 3 m. Suitable spawning substrate

below 8 kcfs was found at a number of locations in Marble Canyon (Table 6.1), with the majority of larger sites located between the confluence of Nankoweep Creek and Kwagunt rapid. The single largest potential spawning site was associated with a mid-channel gravel/cobble bar at river mile 1.6. This site was approximately 2,500 m² and was located at the upstream end of a riffle where hyporeic flows would be maximized. The vast majority of the other sites with appropriate grain sizes in Marble Canyon were located at the downstream end of riffles or small rapids at depths of 3-10 m (at a discharge of ca. 9 kcfs). Pool-tailouts located at the upstream end of debris fans in Marble Canyon were almost always composed of either large cobbles and sand, or large boulders. We did not observe any redds above or below the minimum daily flow elevation during the June survey, however few redds in Glen Canyon were still present by this date (Fig. 2.4).

Table 6.1. Locations with suitable gravel for rainbow trout spawning in Marble Canyon above and below 8 kcfs based on April and June surveys in 2004. Site locations are from the GCMRC shoreline habitat coverage with the identifier denoting shoreline type (sand bar=SB; cobble bar=CB; debris fan=DB; talus=TA), distance in miles from Lees Ferry, and right (R) or left (L) bank. ‘*’ denotes relatively large sites with over 500 m² of suitable spawning habitat.

< 8 kcfs	>8 kcfs
CB1.7R*	DB17.2R
TA5.6R	DB37.0R
DB37.6L	DB35.5L
CB49.1L	DB37.6L*
CB52.7R	DB39.3R
DB53.5R	
SB54.7R*	
TA55.3R*	

6.2.2 Nankoweep Creek Spawning Habitat, Redd, and Young-of-Year Surveys

Nankoweep Creek was accessible to fish in the Mainstem Colorado River in 2004. The majority of the lower 3 km of the creek was composed almost entirely of highly suitable spawning gravels. Based on an estimated average width of 2 m, the lower 3 km of Nankoweep Creek could support at least a few thousand spawners. We counted a

total of 12 adult rainbow trout and saw 2 redds during the April trip and no redds or rainbow trout were observed in June. Gravels were very loose during the April survey but were completely cemented and immobile during the June survey. Flow in Nankowweep Creek is dominated by snowmelt in the late-winter and early-spring and by groundwater later in the year. The immobile gravel bed observed during the June trip was very likely caused by a higher rate of calcium carbonate precipitation owing to the increase in water temperature. During the April survey, water temperatures were ca. 16-18 C, however water temperatures were lower than the maximum lethal limit of 16 C prior to mid-March (Fig. 6.2). Based on seasonal trends in temperature and gravel quality, spawning In Nankowweep Creek during January and early February would likely produce viable YoY.

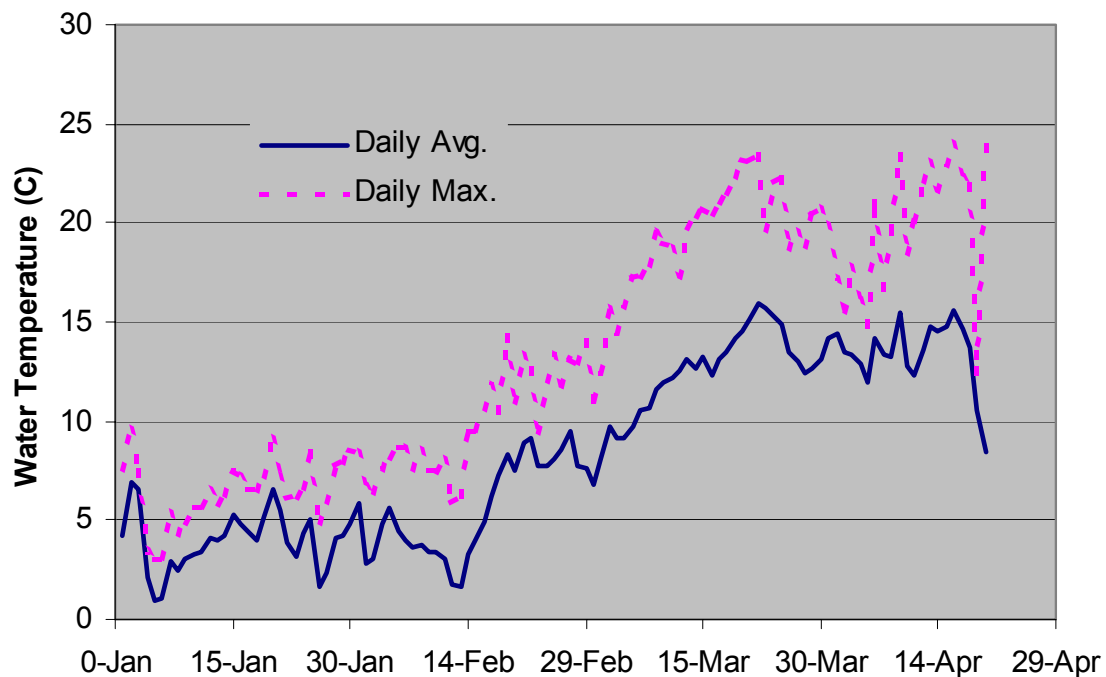


Figure 6.2. Daily average and maximum water temperatures in Nankowweep Creek in 2004. Data provided by GCMRC Downstream Integrated Water Quality Program.

We did not find any YoY rainbow trout in Nankowweep Creek during the April 2004 survey. Very high densities of YoY speckled dace observed during the June survey suggest that the creek is capable of supporting high densities of larval and juvenile fish. It

is possible that rainbow YoY had already left the creek and entered the mainstem by the April survey.

6.2.3 Mainstem Young-of-Year Surveys

Only six YoY trout were captured below Lees Ferry during the April survey. Because of reduced water clarity below the Paria River, comparisons of YoY densities in Glen and Marble Canyon cannot be made for this trip. Water clarity in June and August was very good and similar to that in Glen Canyon allowing for a legitimate comparison of densities in these months. We found very few YoY rainbow trout below Lees Ferry during June or August surveys. Across gear types, we caught 91 YoY from 79 sites between Lees Ferry and the LCR confluence in June, compared to 567 fish from 40 sites in Glen Canyon. In August 2004, we caught 136 fish from 76 sites in Marble Canyon compared to 1,074 fish from 40 sites in Glen Canyon. Across gear types, densities of YoY rainbow trout in Glen Canyon were 12-fold higher than in Marble Canyon in June and 15-fold higher in August (Fig. 6.3). Density of YoY in Marble Canyon was highest in the 15-mile reach immediately below Lees Ferry for both gear types, suggesting that these fish likely emigrated from Glen Canyon. This hypothesis is supported by the temporal trend in backpack electrofishing densities, which showed an increase in density in the first two 15-mile reaches below Lees Ferry in August compared to June. The reach between river mile 45 and 60 had the lowest densities of YoYs of all the reaches below Lees Ferry with only 14 and 4 YoY fish caught in June and August, respectively. This suggests that, although this reach had the greatest amount of spawning habitat in the mainstem and a tributary that could support significant spawning (Nankoweep Creek), these habitats did not produce viable young. If they had, we would have seen an elevated density in this reach relative to others in Marble Canyon where little spawning habitat was found.

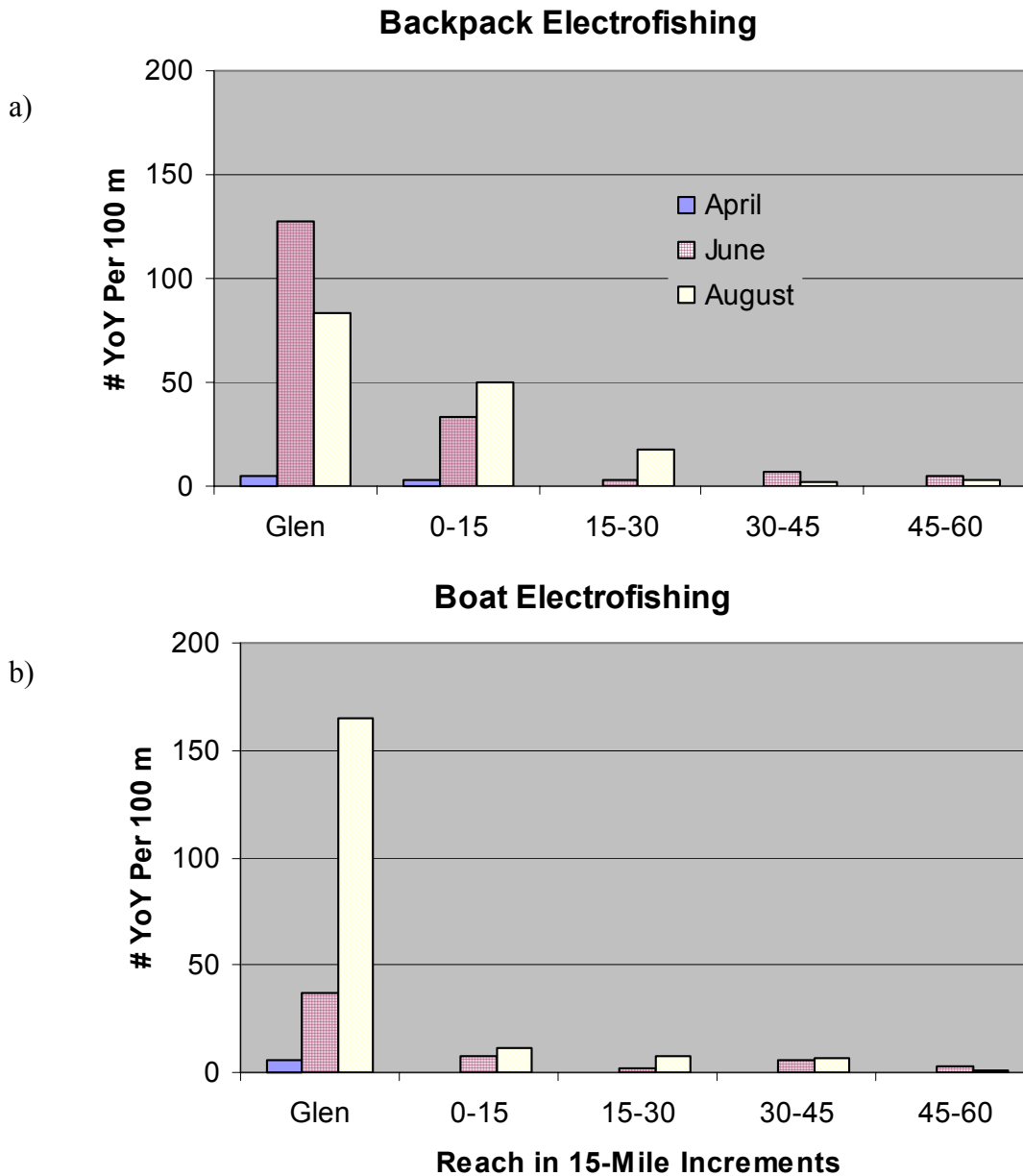


Figure 6.3. Catch-per-effort of YoY rainbow trout by 15 mile reach from Glen Canyon Dam to river mile 60 from samples collected by a) backpack and b) boat electrofishing.

There were no differences in mean size or length-at-age between fish captured in Glen and Marble Canyons. Mean forklength across gear types for YoY captured in June in Glen and Marble Canyons was 38 and 40 mm, respectively. In August the mean size for YoY in Glen and Marble Canyon was 51 and 50 mm, respectively. We attempted to

age all YoY captured in Grand Canyon by counting daily rings on the sagittal otolith because the total number of fish captured was below our target for age samples. A total of 251 fish were captured in Grand Canyon including those caught in April and below the confluence with the Little Colorado River. We successfully aged 244 of these fish which included 8 fish > 100 mm. A logistic growth model based on age-at-hatch explained 85% of the variation in forklength using all samples collected in Grand Canyon (Fig. 6.4, $n=244$, $L_{\infty}=169.2897$, $K=0.0127$, $t_0=169.5977$). This model predicted a much larger length-at-age compared to the model for Glen Canyon because of the sample of 8 fish > 100 mm. Owing to difficulties in ageing larger fish (Section 4.1.2), we did not attempt to estimate the age of fish with forklengths > 100 mm in Glen Canyon. We made a small exception to this rule in Grand Canyon because our sample size was so small. However, when comparing length-at-age models between Glen and Grand Canyon fish larger than 100 mm from the Grand Canyon sample must be excluded from the analysis to make the datasets comparable. When we did this, the logistic model for Grand Canyon explained 78% of the variation in forklength ($n=236$, $L_{\infty}=107.8317$, $K=0.0163$, $t_0=112.3524$) and was very similar to the model for Glen Canyon.

Length-at-age did not appear to be effected by sample location in Grand Canyon, but there were differences across sample dates (Fig. 6.5). Fish captured in August that were between 60-89, 90-119, and 120-149 days from hatch were on average 3, 4, and 12 mm larger than fish captured in June, respectively. Differences in size between the 90-119 and 120-149 day age groups were significant at Type I error rates of 1% and 0.1%, respectively. YoY over 100 mm were captured exclusively in April. These fish were between 210 and 300 days old from hatch and were therefore the progeny of fish that spawned in May and June of 2003.

The back-calculated hatch date distribution for YoY captured in Grand Canyon was indistinguishable from the distribution in Glen Canyon (Fig. 6.6) using the sample periods that were common to both reaches (June and August). These sample periods provided a relative unbiased hatch date distribution for Glen Canyon when compared against the distribution generated from all sample data. This occurred because the June

and August samples cover the vast majority of the interval when newly emerging fish become vulnerable to our sampling gear.

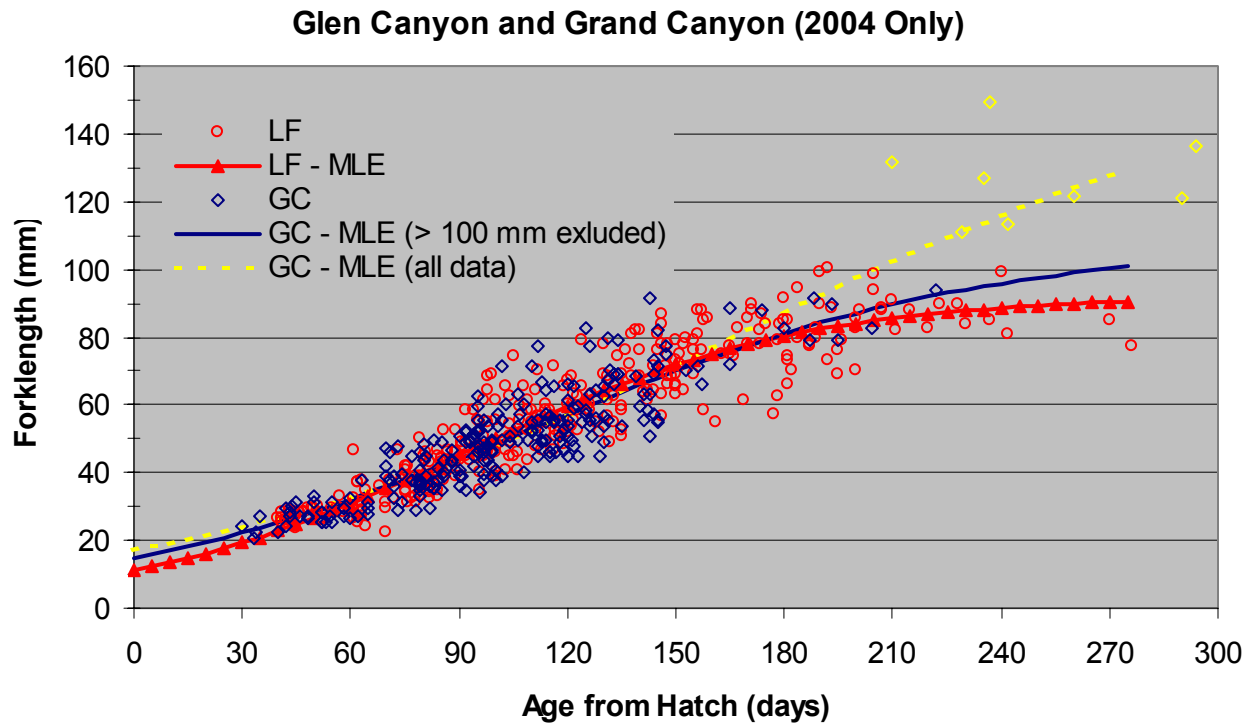


Figure 6.4. Length-at-age for YoY rainbow trout captured in Glen (LF) and Grand (GC) Canyons in 2004 and most likely estimates (MLE) of logistic growth models. Grand Canyon models were estimated using all the data and as well as using data that excluded fish larger than 100 mm to allow comparison with the model for Glen Canyon.

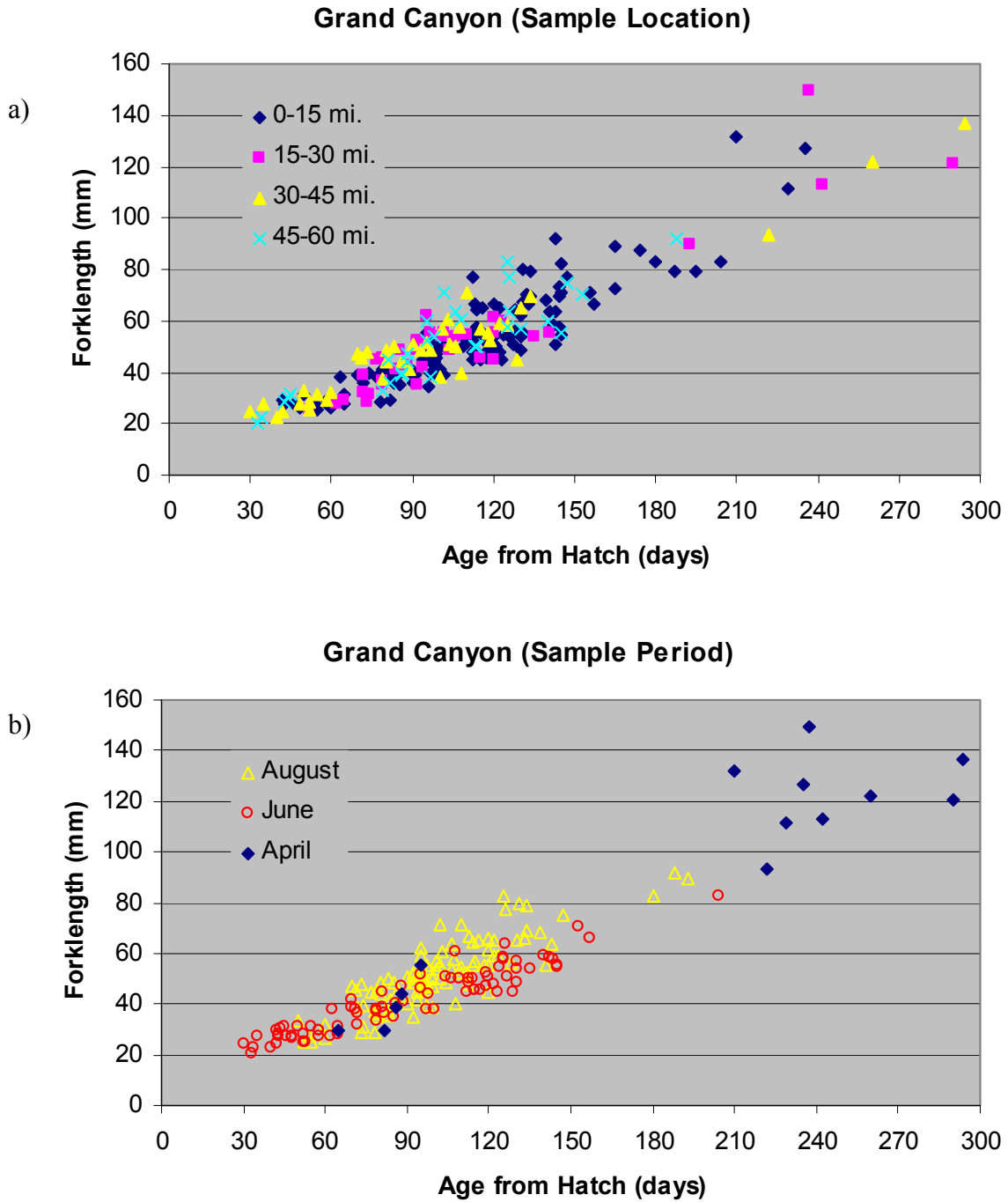


Figure 6.5. Length-at-age for almost all of the fish captured in Grand Canyon in 2004 ($n = 244$ of 251 fish captured) stratified by a) capture location (in river miles from Lees Ferry) and b) sampling trip.

6.3 Conclusions from Marble Canyon Surveys

Relative to Glen Canyon, we observed very little rainbow trout spawning habitat in the mainstem Colorado River in Marble Canyon during our June 2004 survey. There was virtually no spawning habitat above 8 kcfs and most of the potential spawning areas that were identified below 8 kcfs were very deep. We conclude that the efficacy of dewatering rainbow trout redds in Marble Canyon through manipulation of flows from Glen Canyon Dam is extremely low. Flows that increase fine-sediment storage in main channel environments are more likely to limit mainstem spawning or reduce incubation survival. The densities of YoY rainbow trout in Marble Canyon in 2004 were extremely low relative to Glen Canyon. If this observation continues to hold, altering flows to destabilize nearshore habitats in Marble Canyon in an effort to reduce rainbow trout YoY survival is futile because there are so few fish to affect.

There is some evidence that the YoY caught in Marble Canyon in 2004 originated in Glen Canyon. The downstream gradient in YoY density in Marble Canyon coupled with the increase in their downstream distribution between June and August is the expected pattern from a downstream dispersal process (Fig. 6.3). The similarity in length-at-age (Fig. 6.4) and length back-calculated hatch date distributions (Fig. 6.6) between fish captured in Glen and Marble Canyons supports the notion that these fish hatched in a common area. We caution that there is reasonable uncertainty regarding this conclusion. Only tagging studies will provide irrefutable evidence for downstream dispersal, however the feasibility of tagging sufficient numbers of juvenile fish for such an assessment is quite low.

The extremely low density of YoY rainbow trout in Marble Canyon that we observed in 2004, indicates that there was little successful reproduction in this reach or in Nankoweep Creek. This is somewhat surprising, as the relatively clear-water conditions in Marble Canyon since 2000 would support relatively good spawning and incubation conditions compared to previous years where fine-sediment inputs from the Paria River

were higher. Across gear types, densities of YoY rainbow trout in Glen Canyon were 12-fold higher than in Marble Canyon in June and 15-fold higher in August. In contrast, adult densities in Glen Canyon are about 5-fold higher than in Marble Canyon. Assuming equal relative catchability between YoY and older fish in Glen and Marble Canyons during clear-water surveys, the difference in the ratio of YoY-to-adult densities suggest that either: 1) there is not enough juvenile production in Marble Canyon to support the current adult population and if this continues the population will decline; or 2) the Marble Canyon population will remain relatively constant, and the lower ratio of YoY-to-adults simply reflects a higher survival rate in Marble Canyon. The latter hypothesis seems implausible. By combining our YoY survey data with the adult CPE data from AGF, there are approximately 2.5-3 YoY caught for every 1 adult in Glen Canyon compared to a ratio of 1-to-1 in Marble Canyon. It is difficult to believe that YoY-to-adult survival rates are 3-fold higher in Marble Canyon as both rainbow trout habitat and food availability are very likely higher in Glen Canyon.

There are three possible explanations why we observed very limited successful reproduction of rainbow trout in Marble Canyon in 2004. First, if fish capable of maturing were concentrated in the mechanical removal reach (Kwagunt rapid to river mile 72), the majority of the spawning stock could have been removed prior to the spawning season in 2004. This hypothesis is improbable as the spatial trend in adult rainbow trout below Lees Ferry shows higher densities upstream of the removal reach both before implementation of mechanical removal and during the 2004 spawning season (Fig. 6.1b). A second hypothesis is that spawning habitat in the mainstem below Lees Ferry is underutilized because it is relatively ephemeral compared to habitat in Glen Canyon. Occasional sediment inputs from the Paria River would bury clean spawning gravels. Generally, there is a high degree of homing by spawning rainbow trout to at least a tributary scale (Scott and Crossman 1973) and otolith and genetic studies have shown that salmonids (chinook and steelhead) can home to distinct incubation habitats (Quinn et al. 1999, Bentzen et al. 2001). Potentially strong fidelity to spawning sites provides a mechanism to explain why the ephemeral spawning habitat below the Paria River is underutilized relative to the consistently available spawning habitat in Glen Canyon. The

same argument applies to spawning in Nankoweep Creek, where large floods have temporarily blocked access from the mainstem and resulted in high inter-annual variability in the quality of suitable spawning substrate. A third hypothesis for the apparently low reproductive success of rainbow trout in Marble Canyon in 2004 is that reduced condition of adult fish lowered the rate of sexual maturation. Reductions in the rate of sexual maturation associated with reduced somatic growth and lower condition factor have been documented for other salmonids (e.g., Duston et al. 2003, Duston and Saunders 1998). The rate of sexual maturation for fish in Glen Canyon was low in 2000 when condition factor was near its historical minimum of 96-97 (B. Persons, pers. comm.). McKinney et al. (1999) documented a strong inverse relationship between density and condition factor in Glen Canyon. Densities of rainbow in the mainstem near the LCR during between 1996 and 2000 were 3-fold higher than densities in 1990-1995. It is possible that this increase in rainbow trout density in Marble Canyon has reduced the rate of sexual maturation resulting in the very low YoY densities observed in 2004. Further analysis of condition and maturation data in Glen and Marble Canyons is required to strengthen or refute this hypothesis.

While data from our YoY surveys provides good evidence that there was little successful reproduction in Marble Canyon in 2004, our results cannot be used to determine the origin of the current adult population of rainbow trout. It is possible that these fish were spawned and hatched in Marble Canyon and that the low densities of YoY we observed in 2004 was a relatively unique occurrence. Continued documentation of low YoY densities in Marble Canyon over the next few years, combined with observations of a constant or increasing adult population above the mechanical removal reach, would provide good evidence that population is being supported by downstream dispersal from Glen Canyon. Alternatively, if downstream dispersal is not a significant process, and if the lack of significant local reproduction in Marble Canyon continues, the rainbow trout population in this reach should decline substantially over the next few years.

7.0 References

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